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ILLINOIS BIOLOGICAL MONOGRAPHS

Vol. XII

January, 1929

No. 1

MORPHOLOGICAL STUDIES OF THE GENUS CERCOSPORA

WITH FOUR PLATES

BY
WILHELM GERHARD SOLHEIM

Price \$1.00

PUBLISHED BY THE UNIVERSITY OF ILLINOIS
UNDER THE AUSPICES OF THE GRADUATE SCHOOL
URBANA, ILLINOIS

UNIVERSITY OF ILLINOIS STUDIES PUBLISHED

ILLINOIS BIOLOGICAL MONOGRAPHS

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TABLE OF CONTENTS

Nos.	PAGES
1. Morphological Studies of the Genus <i>Cercospora</i> . By WILHELM GERHARD SOLHEIM	1
2. Morphology, Taxonomy, and Biology of Larval Scarabaeoidea. By WILLIAM PATRICK HAYES.....	85
3. Sawflies of the Sub-family Dolerinae of America North of Mexico. By HERBERT H. ROSS.....	205
4. A Study of Fresh-water Plankton Communities. By SAMUEL EDDY.....	321

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DISTRIBUTED
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WITH FOUR PLATES

BY
WILHELM GERHARD SOLHEIM

Contribution from the
Botanical Laboratories of the University of Illinois

THESIS

SUBMITTED IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE
DEGREE OF DOCTOR OF PHILOSOPHY IN BOTANY IN THE GRADUATE
SCHOOL OF THE UNIVERSITY OF ILLINOIS

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TABLE OF CONTENTS

Introduction	
History	7
Materials and Methods	8
Acknowledgment	9
Morphology	
On the Host	10
Mycelium	10
Condiophores	10
Conidia	12
In Culture	12
Life History	16
Taxonomic Affinities	18
Division of Cercospora into Sections	22
Systematic Arrangement of the Genus	25
Key to Sections of Cercospora	26
Section I	27
Section II	29
Section III	30
Section IV	31
Section V	40
Section VI	42
Section VII	47
Section VIII	48
Section IX	50
Section X	51
Section XI	52
Section XII	53
Section XIII	54
Section XIV	56
Section XV	56
Section XVI	57
Section XVII	58
Section XVIII	59
Section XIX	60
Section XX	62
Section XXI	64
Didymaria (Corda) <i>emend.</i> Solheim	64
Host Index	68
Species Index	72
List of New Names and New Combinations	73
Bibliography	74
Explanation of Plates	77

INTRODUCTION

HISTORY

The genus *Cercospora* was established by Fresenius in 1863, the name being derived from the Greek *kerkos*—a tail, and *spora*—a spore. Fresenius did not, however, distinctly characterize the genus but merely listed four species with descriptions, confining his remarks concerning the genus to a footnote to the description of *C. apii* Fresen., the type species. In the footnote he states: "Dieser Pilz, welchen ich von Herrn Fuckel mitgetheilt erhielt, war unter den beschriebenen Gattungen nicht wohl unterzubringen. Ich belegte ihn daher wegen der mitunter lang ausgezogenen Schwänze der Sporen mit obigen Gattungsnamen, 'Cercospora' . . . Cylindrische Sporen kommen eigentlich hier nicht vor und von den Fusisporien weichen die Cercosporien in der Beschaffenheit der sporentragenden Fäden und der Sporenformen selbst ab." These are the only generalizations made by Fresenius. He states that it is not advisable to further describe the genus until there is a better understanding of this group of fungi. The limits of the genus are, therefore, not specifically defined but are left for later interpretation.

Cooke (1875) described the genus *Virgasporium*, listing two species, *V. maculatum* Cooke and *V. clavatum* (Gerard) Cooke. Later, accepting Saccardo's statement that this genus was identical with *Cercospora*, Cooke (1875a) transferred the two species to that genus.

Since the establishment of the genus, numerous species have been added by various workers. Saccardo, in volumes one and two of *Micheliá*, mentioned and described fifty-eight species. He illustrated many of these and others in his *Fungi Italici*. Ellis and Everhart (1885–1888) described many new North American species. Descriptions of numerous Alabama species were given by Atkinson (1891). The last two papers also contain rather detailed descriptions and discussions of the genus and its limits. In 1900, Carver published a list of the *Cercosporae* of Macon Co., Alabama, adding several new host plants for already described species. Of the other workers, Lindau (1910) deserves special mention for enumerating with descriptions, discussions, and some illustrations all the central European species known at the time of his work.

Besides these works, a large number of local lists of fungi have recorded and described *Cercosporae*, so that the genus is at present quite formidable. Saccardo, in the *Sylloge Fungorum*, lists approximately five hundred species.

Since the issue of the last volume of this work containing Cercosporae, many new species have been added, so that the total number of species is now much larger.

The early concepts of the genus *Cercospora* included all the Moniliaceae and Dematiaceae with well-developed conidiophores and long filiform conidia. As such, it was very close to *Ramularia* (of the type of *R. tulasnei* Sacc.), being separated from it principally on the basis of conidial length. When Saccardo constructed his system of classification based primarily on color, it became necessary to separate the hyaline from the colored forms. Saccardo (1880), therefore, established the genus *Cercosporella* to include all hyaline Cercosporae. Spegazzini (1910) further split up the genus in establishing the genus *Cercosporina*, which he made to include all Cercosporae with colored conidiophores and hyaline conidia.

Ellis and Everhart grouped the species for convenience into sections based on presence or absence of color in the conidiophores and on the nature of the spots produced. They did not, at that time, recognize the genus *Cercosporella* of Saccardo.

No other attempt has been made to divide the Cercosporae into sections. Von Höhnelt (1902) has suggested that the genus may readily be divided on the basis of the manner of emergence of the conidiophores, i.e., whether they protrude through the stomata or rupture the epidermis and cuticle. Lindau, however, does not consider this a good divisional character, stating that the manner of emergence is undoubtedly due to the nature of the host rather than to any fundamental difference in the *Cercospora* species.

It has generally been held that the *Cercospora* species are fairly strict in their parasitism, each being limited to one host species or to a few very closely related host species. For this reason, use has been made of host reaction coupled with size of conidiophores and conidia as primary characters for species delimitation. In a recent taxonomic study of the genus, Welles (1924, 1925) indicates that host range is not limited to any family or group of plants and that the characters just mentioned are greatly modified by the various hosts. He concludes that "the only valuable taxonomic criteria which have presented themselves for use in separating various species of *Cercospora* are physiological behavior on artificial media and extent of parasitism."

MATERIALS AND METHODS

The studies of the fungi of this investigation were all made from dried specimens from the University of Illinois Herbarium, from various exsiccati and a few secured from the Royal Botanic Garden at Kew, the New York Botanical Garden, and the Missouri Botanical Garden. They were prepared for study by boiling in a sodium hydroxide solution to soften

them and to remove the coloring matter of the host. They were then boiled in water to remove the sodium hydroxide.

The measurements recorded for conidia, conidiophores, and mycelium, with the exception of measurements of length, were all made with the oil immersion lens. Measurements of length were made with the 4 mm. objective. Whenever possible they were made for both dry and boiled material. Diameter of conidia was measured at both the base and tip. Conidial measurements are recorded in the descriptions as follows; length \times diameter of base \times diameter of tip. When any single character requiring numerical expression is described with three figures, e.g., 20–150–225, the first number indicates the minimum observed; the second, the usual maximum; and the last, an occasional maximum.

Color, when not readily assignable to a specific category, was determined by comparison with the Ridgway (1912) color standards and the nomenclature of them employed. The color of conidia and conidiophores was determined from water mounts of the dried material, while that of the mycelium was determined from material prepared as indicated above. These color determinations were always made by transmitted daylight. Artificial light was never used.

A preliminary survey of over one hundred species was made in order to acquire some general concepts as to variability of form in *Cercospora* and to aid in selection of species for a more detailed study. Those studied in detail are listed in the sections with full descriptions. Those not yet studied in detail are listed with citation to place of original description and the source of the specimen examined. In the latter case, species determinations were accepted as recorded.

Citations to literature following the specific names of described species include publications of descriptions and of new host plants. Illustrations are also listed. While these lists undoubtedly are not in all cases complete, an effort has been made to make them complete. It is hoped that all the important references have been secured.

ACKNOWLEDGMENT

The work upon which this paper is based was done in the plant pathology laboratory of the University of Illinois under the direction of Professor F. L. Stevens. The writer is greatly indebted to Professor Stevens for the suggestion of the problem and for kindly criticism and suggestions offered during the course of the investigation.

MORPHOLOGY

ON THE HOST

MYCELIUM

The mycelium of the Cercosporae consists of very fine to coarse, fairly regular to very irregular, septate hyphae which for the most part ramify the host tissue. Not infrequently, however, the mycelium is produced externally as well, and then the external threads take their origin in two ways. Usually they arise from the internal mycelium and emerge through the stomata, as in *C. condensata* Ell. & Kell. and *C. petersii* (B. & C.) Atk., but they may also arise directly from the conidiophores, as in *C. portoricensis* Earle. The latter procedure is not common.

In color, the mycelium varies from hyaline or subhyaline, as in *C. acalyphae* Peck, to olivaceous or olive-brown, as in *C. tuberosa* Ell. & Kell. Usually it varies from hyaline or subhyaline to some shade of brown, as in *C. apii* Fresen. The mycelium, when young, is as a rule colorless or only slightly colored. As it becomes older, it may remain so, or pigments may be produced so that the old mycelium not infrequently is a deep shade of brown.

Frequently, if not always, the old mycelium in the dead host tissue produces sclerotia-like bodies, or the cells of the mycelium thicken, become heavy-walled, and are transformed into chlamydospores or chlamydospore-like structures. These serve as a means of over-wintering the fungus.

When the fungus has advanced to the stage at which the asexual reproduction occurs, there are formed or already have been formed, at various points on the mycelium within the host tissue, more or less compact bodies, or stromata. The stroma may consist of a large, compact, tuberculate, pseudoparenchymatic structure, as in *C. smilacina* Sacc. (Fig. 10) and *C. tuberosa* Ell. & Kell. (Fig. 12). More commonly, however, it is made up of rather loosely to fairly compactly interwoven hyphae not of a pseudoparenchymatic nature, e.g., *C. apii* Fresen. (Fig. 1) and *C. cercidicola* Ell. (Fig. 5). In some cases the stroma may be almost completely lacking or made up of only a few more or less loosely associated cells, e.g., *C. ferruginea* Fckl. (Fig. 6) and *C. acalyphae* Peck (Fig. 2). Intermediate forms of all degrees exist between the types just cited.

CONIDIOPHORES

The conidiophores arise from the stromata described above and emerge from the host tissue either through the stomata or by rupturing the epider-

mis. Both types of emergence may be found in a single species, the point at which the conidiophores emerge apparently being largely determined by the position of the stroma. When a species produces an external mycelium, the conidiophores may also be produced in an effuse manner on it, e.g., *C. portoricensis* Earle (Fig. 13).

The number of conidiophores arising from a single stroma may be few or many. As a result, they are produced in loose to dense, more or less divergent tufts. In *C. cercidicola* Ell. (Fig. 5) and *C. petersii* (B. & C.) Atk. (Fig. 11) the tufts are coremioid. Rarely are the conidiophores solitary, and in no case have they been observed to be so throughout. In *C. carotae* (Pass.) Solheim, they are sometimes solitary but they are also produced in very loose tufts.

Considerable variation exists in the size, markings, and color of the conidiophores. They may be continuous or septate, straight or flexuous, geniculate, denticulate, hyaline or of various shades and tints of brown up to blackish-brown. The denticulations, geniculations, and flexuous conditions are produced by the manner of growth of the conidiophores while bearing conidia. The conidia are borne acrogenously, although at times they appear lateral because of the development of a lateral branch just below the point of attachment, which pushes the terminal point of the conidiophore to the side, while the conidium is still attached. The branch soon proceeds to develop another conidium, and a single conidiophore may continue to develop in this manner, producing several conidia. The general shape and markings of the conidiophore are dependent on the degree to which the branch succeeds in pushing the apical point of conidial attachment to the side, and on the rate of growth of the conidiophore as compared with the rate of production of conidia. If the apex with its scar is completely turned to one side, the conidiophore will be nearly cylindrical, with scars distributed along its sides. The scar may not be much displaced and the branch then diverges from the general direction so as to produce a geniculation, the scar being shouldered. When a second conidium is produced, the next branch usually arises on a different side, most frequently the opposite side; consequently, the divergence is in a different direction, giving a somewhat zigzag appearance. At times, the branch is set a little below the apical scar, so that the scar, when pushed to the side, becomes denticulate.

The conidiophore, as a result of this type of branching, is sympodial. Such a conidiophore is usually spoken of as being simple when pertaining to this group of fungi. Besides this sympodial branching, monopodial branching is also found in many species, e.g., *C. ferruginea* Fckl. (Fig. 6). Only a few of the conidiophores of a given species may produce this latter type of branch, but in other species a very high percentage may be thus branched. Usually there is no definite arrangement of the monopodial branches. Most

commonly they are irregularly alternate. More rarely they are opposite, being subtended by a terminal conidial scar, e.g., *C. cercidicola* Ell. (Fig. 5). Again, they may be both alternate and opposite as in *C. illinoensis* Barth. (Fig. 8).

CONIDIA

The conidia of *Cercospora* are of several distinct morphological types. Certain species, e.g., *C. acalyphae* Peck (Fig. 2), have conidia of which the point of attachment is as wide as the greatest diameter of the conidium. From or near the base, the conidium gradually tapers to the tip. For this type the term acicular is suggested. In other species, the point of attachment is narrower than the greatest diameter. These are termed acicular-obclavate or narrowly obclavate if they taper gradually as in the above type, e.g., *C. smilacina* Sacc. (Fig. 10), or merely obclavate or abruptly obclavate if there is an abrupt tapering directly above the greatest diameter, e.g., *C. ferruginea* Fckl. (Fig. 6). In the last two types, the greatest diameter of the conidium is very near its base. If the greatest diameter is at or near the center, the conidia are fusiform as in *C. pastinacae* (Sacc.) Peck (Fig. 14). In other species the conidia are cylindrical, e.g., *C. althaeina* Sacc. (Fig. 3).

The conidium, in its development, first appears as a small, oval, elliptical, clavate or cylindrical body. As it grows, it elongates and assumes one of the forms described above. The conidia are usually borne singly but may be catenulate, as in *C. catenospora* Atk. They are usually septate and may or may not be constricted at the septa. They are straight or curved and vary in color from hyaline or subhyaline to various shades and tints of yellow or brown, such as olive-brown, Dresden brown and Prout's brown.

IN CULTURE

In pure culture, individual *Cercospora* species react quite differently. Duggar (1899), working with *C. beticola* Sacc., found that it did not produce conidia in culture on artificial media. The same has been observed for *C. concors* (Casp.) Sacc. by Jones and Pomeroy (1907), for *C. fusca* Rand by Rand (1914), for *C. bolleana* (Thüm.) Speg. by Higgins (1920) and for *C. lythracearum* Heald & Wolf by Wolf (1927). Garman in 1920 found that *C. brunckii* Ell. & Galw. grew well on several media but that it did not readily produce conidia. On the other hand, several other species have been shown to produce conidia abundantly in culture. Among these are *C. personata* (B. & C.) Ell. cultured by Wolf (1914), *C. medicaginis* Ell. & Ev. studied by Hopkins (1921), *C. apii* Fresen., studied by Klotz (1923), *C. microsora* Sacc. studied in culture by Klebahn (1918) and several Philippine species cultured by Welles (1925). All of the above workers

found that the particular species grew on most media tried, and all, with the exception of Welles, report growth as being slow, only a few millimeters or at most a few centimeters growth being produced in several weeks. Welles, on the other hand, reports very rapid growth in artificial culture for the five species studied by him.

In the present investigation, attempts were made to artificially culture various species of *Cercospora*. Only two species, however, were isolated that produced conidia on artificial culture media. These were *C. ampelopsidis* Peck and *C. illinoensis* Barth. Other fungi, supposedly *Cercospora* species, were isolated from various hosts, but because they failed to produce conidia their identity could not definitely be determined without infection studies which circumstances did not permit.

The two species that were isolated grew on all media tried. The media employed were selected with the view of varying the carbohydrates to observe any effects this might have on the morphology and color. Several standard synthetic media were, therefore, used as well as some specially prepared. A chemical base agar was made up according to the formula given by Stevens and Hall (1909). This was used alone or in combination as follows: chemical base agar + glucose, chemical base agar + starch, and chemical base agar + sodium asparaginate. Besides these media potato dextrose agar, bean pod agar, corn meal agar, and agar were used.

The morphology of *C. ampelopsidis* Peck in culture varied little from that in the host. In both cases a rather fine and a coarse beaded mycelium was produced. However, in culture a much greater amount of the coarse beaded type was produced than in the host. It is quite possible that this difference is due to the age of the specimens examined as compared with the age of the cultures. A physiological old age may possibly be reached much sooner in culture than in the host, due to attendant conditions. The cells of the coarse mycelium were chlamydospore-like and perhaps are the means by which this fungus overwinters. The conidiophores do not differ essentially in the two cases. The most striking difference was found in the conidia. In artificial culture they were catenulate, whereas they are not so in nature. Their shape is somewhat altered in culture, due to this fact, the conidia in culture being subcylindrical, while in nature they are abruptly obclavate.

The growth of this fungus in culture was rather slow, being most rapid on potato dextrose agar. No striking differences were noted in the morphology on the various media. The finer mycelium was much the same throughout. The coarse mycelium varied somewhat, being decidedly beaded on some media and not so on others. On the chemical base agar + glucose, much thicker cell walls were produced in the coarse mycelium than on any of the other media. The conidiophores were much the same throughout but were rather poorly developed on the chemical base agar + glucose. On

this agar, conidial production was also rather limited and the conidia were rarely catenulate. The color of the fungus varies considerably with age. When young the various structures are hyaline to subhyaline. As the fungus becomes older, pigments are produced which are of various shades of brown, olive-brown and olivaceous, depending somewhat on the medium. While the color varied somewhat in intensity on the different media these differences were not very pronounced. The coloring material was in part diffused throughout the medium.

The conidiophores arose only from the submerged mycelium. They were readily distinguished from the mycelium, appearing as definite morphological units.

C. illinoensis Barth. grew most rapidly on potato dextrose agar and on corn meal agar, from the standpoint of colony diameter. However, if density of growth is also considered, then growth was best on potato dextrose agar.

Some variability in the mycelium occurred in the different media, especially from the standpoint of the production of a coarse, irregular, heavy-walled mycelium which was produced only in some of the media. Conidiophores and conidia were produced abundantly on all media except potato dextrose agar and chemical base agar+starch. The conidiophores arose from the submerged mycelium only. Conidia were produced most abundantly in pure agar. They also appeared to vary less in size and irregular constriction in the latter medium than was the case in the other media. Considerable variability in color was noted on the various media. The color variation was primarily one of degree, varying from dilute light olivaceous to dark Prout's brown. The darkest color was produced on the corn meal agar and chemical base agar+glucose. The coloring material was not confined to the fungus hyphae but was diffused throughout the medium as well.

No striking differences were noted in the morphology of this fungus in pure culture and in the morphology on the host. The conidia in culture were more nearly cylindrical than in nature. The conidiophores appear in general to be effused in culture. While they were loosely tufted in potato dextrose agar they were abnormal and only sparingly produced, so that this condition is perhaps not normal. Other differences were of no importance.

From the cultural studies here made, it is indicated that *Cercospora* species that complete their life-cycle in pure culture do so in a similar manner as in nature with very little variation in morphologic structure. Welles (1925) in his culture studies of several *Cercospora* species, states that the conidiophores are merely extended mycelial threads and that it is impossible to distinguish them from the mass of mycelium in pure culture. In the present case, no difficulty was found in distinguishing the conidio-

phores in pure culture of the two species studied. They may, at times, be rather difficult to observe, due to the abundance of mycelium which tends to obscure them. That the conidiophores of *Cercospora* are definite morphological units is also borne out by the fact that in nature, when they are effused on an external mycelium, they are quite distinct, and conidial production is limited to these structures. The conidia, in these cases, are not produced in a haphazard manner on the external mycelium.

Klotz (1923) in his culture study of *C. apii* Fresen. states that the pigment produced by this fungus was confined to the hyphal threads. This is apparently not the case with all *Cercosporae*, as in the two studied here the coloring material was diffused through the medium as well.

That color is of little value as a taxonomic character with respect to this group of fungi where differences in color consist primarily in a difference in intensity of a series of browns, is indicated by the comparative ease with which it may be varied by employing different culture media. Color may, however, be fairly constant under different conditions, as only slight variations were produced in *C. ampelopsidis* Peck. On the other hand, wide variations in color were produced in *C. illinoensis* Barth. in the different media.

LIFE HISTORY

The Cercosporae are, for the most part, leaf parasites which produce definite, necrotic spots. Not in all cases, however, is their growth limited to the leaves. Frank (1897) states that *C. beticola* Sacc. grows on all parts of the beet plant that are above the soil. Other examples are *C. medicaginis* Ell. & Ev. which grows on the leaves, leaf petioles and seeds of *Medicago maculata* Willd., *C. acalyphae* Peck growing on the leaves and stems of *Acalypha ostryaefolia* Riddell, *C. coffeicola* Berk. & Cooke growing on fruits, twigs and leaves of *Coffea* sps., *C. caulicola* Wint. growing on the stems of *Asparagus officinalis* L., and *C. lythracearum* Heald & Wolf on fruits and leaves of *Punica granatum* L.

Infection of the host by the parasite is usually brought about, after the germination of the conidia, by infecting hyphae which gain entrance through the stomata. This type of infection has been observed for *C. beticola* Sacc. by Pool and McKay (1916) and for *C. apii* Fresen. by Klotz (1923). It has also been observed for several of the species studied in this investigation.

With respect to the manner of conidial germination Atkinson (1891) states as follows: "The conidia germinate readily in an abundance of moisture, a germ tube being put forth by any or all the cells. In my observations, and they have extended over several species, usually the cell first to produce a germ tube is the basal cell, and the primary direction of this tube is in a line parallel with that of the conidium but in an opposite direction from the apex. This is not universal, but occurs in such a great majority of the cases as to be worthy of note." This manner of germination has also been observed to be most prevalent for the species in which germination of conidia was seen in this study. A notable exception occurred in *C. sordida* Sacc. In several of the specimens of this fungus that were examined, germinating conidia were present in great abundance. The conidia germinate at any point. If the conidia, however, happened to be lying over the stomata or just at the side of a stoma, then the germ tube always arose from the point closest to the stoma. In this species and in *C. smilacis* Thüm. conidia were observed occasionally to produce conidiophores as a direct result of their germination.

The Cercospora parasite, as it penetrates the host tissue, in most cases causes the death of the affected part. Its action, however, is more or less limited, and the result is usually the production of a definite spot, the size

of which depends largely upon the efficiency of the host in combating it or upon the ability of the fungus to overcome mechanical obstructions such as veins. Several of these spots may be present, their form varying from circular to angular to irregular. They are variously colored. In some cases the spots are indefinite, the fungus being diffused in patches over the leaf surface.

After a period of incubation, conidiophores and conidia are produced. This period undoubtedly varies somewhat for the different species. Pool and McKay (1916a) have shown it to be from 11 to 13 days for *C. beticola* Sacc. The conidia produced at this time serve as a source of added infection and also for spreading the fungus. They are disseminated by wind, water, insects, etc.

Mycelium and sclerotia, in the old dead portions of the host, perhaps serve as the primary means of overwintering these fungi. This has been shown to be the case in *C. apii* Fresen. by Klotz (1923) and in *C. beticola* Sacc. by Pool and McKay (1916a). McKay and Pool (1918) have also shown that *C. beticola* Sacc. overwinters in the infected crowns of stored roots, or that the conidia may overwinter on the beet seed balls. Hopkins (1921) states that *C. medicaginis* Ell. & Ev. is borne as mycelium on the seeds within the burs. *C. personata* (B. & C.) Ell. according to Wolf (1916) overwinters on the leaves and seeds.

In the spring when conditions are suitable the overwintered mycelium and sclerotia produce conidiophores, the conidia of which serve as the means of infection of the new crop.

This, as far as is known, completes the life history of the majority of the Cercospora species. Some, however, are known to possess a Mycosphaerella perfect stage. These are:

C. cerasella Sacc. = *Mycosphaerella cerasella* Aderhold (1900).

C. microsora Sacc. = *Mycosphaerella millegrana* (Cooke) Schroet. The relationship was proven by Klebahn (1918).

C. bolleana (Thüm.) Speg. = *Mycosphaerella bolleana* Higgins (1920).

C. lythracearum Heald & Wolf = *Mycosphaerella lythracearum* Wolf. The relationship of these two forms is not absolutely proved. Wolf (1927) states: "The relationship of conidial and perithecial stage is evidenced (1) by their occurrence in due time in the same lesions, (2) by the similarity of cultures from conidia and ascospores, and (3) by the fact that a number of Cercosporas are known to possess a Mycosphaerella stage."

Several other connections with Mycosphaerella have been reported for various Cercospora species. None of these, however, have been proved. Of the forms above mentioned *C. bolleana* (Thüm.) Speg. and *C. lythracearum* Heald & Wolf produce spermagonia.

TAXONOMIC AFFINITIES

Cercospora, according to the system of classification now followed, belongs to the group of Fungi Imperfecti known as the Hyphomycetes or Moniliales. The main characterization of the genus has been based on the shape of the conidia, which are vermiform or filiform, and the presence of color in the conidiophores. This places the genus in the family Dematiaceae, which is separated from the Moniliaceae merely on a color basis. That this has led to an unnatural grouping is quite evident. Atkinson (1891) in discussing the affinities of *Cercospora* and *Ramularia* states: "Here we encounter one of the difficulties of the artificial system which exists to a great extent in the arrangement of some of the Hyphomycetes, where such genera as *Ramularia* and *Cercospora*, structurally very closely related to *Cercospora*, are made to do duty in an entirely different family."

If the color barrier which now separates the Moniliaceae from the Dematiaceae, and thus separates these genera, were to be removed and the two families constituted as one family (the Moniliaceae), what would happen? In the first place, genera morphologically closely related, but by the present system widely separated, would fall into more natural groups. In several instances it would undoubtedly result in the consolidation of now separate genera. This step of eliminating color as a primary division character was suggested by von Höhnelt in 1923. In his system, covering the Sphaeropsidales, Melanconiales, Stilbaceae, and Tuberculariaceae, color as a character has been used only secondarily.

That color is not constant, and therefore an unreliable character, has been shown by several workers. Stevens (1922) and Ravn (1900) have noted variations in color in *Helminthosporium* species when grown on various media. Young and Bennett (1922) found that *Fusarium radiculicola* Woll. was colorless in Richard's solution and pink in the same solution when the potassium nitrate was replaced by calcium nitrate. Bessey (1904) produced changes in color in *Fusarium* species by varying the hydrogen ion concentration of the medium. Similarly, Milburn (1904) varied the color of several *Hypocrea* species. He also changed the color of these fungi by varying the osmotic value of the medium. Milburn further showed that *Aspergillus niger* van Tieg. produced a yellow pigment which in the light quickly became gray or black. Stevens and Hall (1909), by varying the carbohydrates of the media employed, secured marked changes in the color of various fungi. In *Volutella fructi* Stev. & Hall sufficient differences

were secured to shift the fungus from the Tuberculariaceae-Dematiaceae to the Tuberculariaceae-Mucedinae. *Colletotrichum carica* Stev. & Hall varied from pale to almost black. Several *Epicoccum* species were colorless on certain media while on other media they were yellow, pink or sometimes black. *Alternaria brassicae* (Berk.) Sacc. varied from hyaline to black on the different media. Similar changes in color to those noted above have been observed in *Cercospora* species by Jones and Pomeroy (1907), Rand (1914), Garman (1920) and Klotz (1923). In the present investigation, as previously stated, the color of *Cercospora illinoensis* Barth. varied from pale to dark brown on different media.

All of these studies clearly show that color can have little value as a character to be used in the classification of this group of fungi. This is further attested for by Arnaud's (1923) procedure, when he proposed the group "Septodiées" of the Hyphomycetes to contain the genera *Diploidium* and *Septoidium*, as these genera will not fit into the Moniliaceae nor the Dematiaceae, for these fungi may be colored or hyaline in the same species and they include types which are not separable genetically. That color is of little value is further indicated by Ellis and Everhart (1885) who have listed six species of *Cercospora* with hyaline conidia and conidiophores. Again, von Höhnelt (1903) shows that the color line has also been ignored with respect to *Ramularia*, and he enumerates 17 species from the Sylloge Fungorum which have colored conidiophores.

From the foregoing, the conclusion is inevitable that color can not be used as a primary character for the separation of families or even of genera in this group of fungi. It is, therefore, proposed to unite the Moniliaceae and Dematiaceae and consolidate as much as possible the forms of the two families. Only *Cercospora* and closely related forms are considered here.

With the color barrier removed, but adhering to the system as employed within the families, we find that the genera *Cercospora*, *Cercosporella*, and *Ramularia* all fall into one group covering two sections of the system, the Phragmosporae and the Scolecosporae. These two sections are not readily separated. To illustrate: Saccardo in 1886 placed the genus *Cercospora* in the Phragmosporae, but in 1899 he transferred it to the Scolecosporae. Lindau in 1900 placed the genus in the Scolecosporae, but in 1910 he put it in the Phragmosporae. Clements (1909) evaded this difficulty by placing the genus in both sections.

Turning to *Ramularia* and *Cercosporella*, we find that these genera have been placed in the Phragmosporae and Scolecosporae, respectively, thus on the basis of their conidia falling into the same sections as *Cercospora*. Further comparisons reveal that *Cercosporella* at least is not morphologically distinct from *Cercospora*. When establishing the genus *Cercosporella*, Saccardo (1880) states that it is a *Cercospora* with hyaline

conidia and conidiophores. It is, therefore, proposed to unite *Cercospora* with *Cercospora*.

A rather unfortunate situation exists with respect to the status of *Ramularia* and *Ovularia*. *Ramularia* was established by Unger in 1833. He, however, did not describe the genus but simply listed two species, *R. pusilla* Ung. and *R. didyma* Ung. Corda in 1842 removed the second species from *Ramularia* and made it the type of a new genus, *Didymaria* [*D. didyma* (Ung.) Schroet. = *D. ungeri* Corda]. This leaves *R. pusilla* Ung. as the type of *Ramularia*. Saccardo in 1881 ignored this fact and put this species in the genus *Ovularia* (*O. pusilla* (Ung.) Sacc.), a genus which he had established in 1880. From this it appears that the genus to properly bear the name *Ramularia* is what today is known as *Ovularia* and further that the group of species known as *Ramularia* has no proper generic name. It is, however, at present inadvisable to make this change in nomenclature. The species *R. pusilla* Ung., around which the question centers, is a very doubtful one, and it is impossible to clear up the problem without further studies.

Wollenweber's concept of *Ramularia* as set forth in 1913 appears at present to be untenable. He identified *Ramularia* with *Septocylindrium*, a genus apparently closely allied to *Fusarium*. Whether *Ramularia* in part is to be considered identical with *Septocylindrium* will depend upon the facts revealed in a study of *R. pusilla* Ung., a study which has not been made. Further, it is certain that many of the species now considered under *Ramularia*, as *R. tulasnei* Sacc., are not even closely related to *Fusarium*. A thorough study of this group of fungi is necessary to determine the ultimate status of the species involved.

The type species of *Didymaria* is *D. didyma* (Ung.) Schroet. This species (Fig. 16) is a *Ramularia* with two-celled clavate conidia. This conidial type is also found in *Cercospora* but is there atypical. It is, therefore, proposed to revise *Didymaria* so that it will include all species with conidiophores of the *Cercospora* type and producing clavate conidia with two or more cells. Here, then, would belong *Didymaria* (*Cercospora*) *effusa* (B. & C.) Solheim, n. comb. The status of the remaining species of *Didymaria*, with oval to obclavate conidia, can not at present be determined but must await the solution of the *Ramularia*-*Ovularia* question. As pointed out by Wollenweber and others, the separation of these forms on the basis of conidial septation is not justified.

Didymariopsis, established by Spegazzini in 1910, is described as a *Didymaria* with colored conidiophores. The type of this genus has not been seen. Following the procedure as set forth above, this will be synonymous with *Didymaria* if the conidia are clavate, or will fall into the group of excluded *Didymariae*, for the present left unattached.

Cercosporina, another genus established by Spegazzini in 1910, is a *Cercospora* with hyaline conidia. This genus, therefore, has occupied a position between *Cercospora* and *Cercosporella*. Since it was proposed to unite *Cercosporella* with *Cercospora*, it follows from the above that *Cercosporina* must also be united with *Cercospora*.

Cercosporidium Earle and *Isariopsis* Fresenius are genera also very closely allied with *Cercospora* and are perhaps not generically distinct. Further studies are, however, necessary to determine the final status of these genera as well as other related genera.

DIVISION OF CERCOSPORA INTO SECTIONS

In the genus *Cercospora*, the morphologic characters which have served to separate species are host reaction and size, shape, and color of conidia and conidiophores. The assumption has been that these characters are fairly constant under varying environmental conditions. If this assumption were true, it might be possible to subdivide the genus into sections based on the size of the conidia and conidiophores.

To determine the value of size as a character for classification of this group of fungi, several specimens of *C. beticola* Sacc. were compared. The results are recorded in the following table:

Specimen No.	Length of Conidiophores in μ			Length of Conidia in μ		
	Minimum	Mode	Maximum	Minimum	Mode	Maximum
1	19.4	38.9	136.1	38.9	90.7	207.4
2	22.6	68.0	136.1			
3	22.6	38.9	71.3			
4	19.4	35.6	55.0	32.9	71.3	136.1

In the description of *C. beticola* Sacc. the length of the conidiophores is given as 40–60 μ , suggesting that there is not a great range in their length. This, as is shown in the above table, is not in accord with the present findings. The conidiophores were found to vary in length from 19.4 to 136.1 μ . The Saccardian description gives the variation in conidial length as 70–120 μ . In the present case, the variation was found to be 32.9–207.4 μ .

The unreliability of conidial and conidiophore length has also been pointed out by Welles (1925) and Overholts (1927). Welles experimentally induced considerable variation in length of these structures in several *Cercospora* species by varying the humidity. He also showed that the size of the conidia and conidiophores, induced through artificial inoculation, varied greatly, depending on the host. The seasonal variation in size of these structures was also considerable. Overholts concludes from a study of *Cercospora* species on *Smilax*, that length of conidiophores is a character of little value.

These studies clearly indicate that division of the genus into groups on the basis of conidial and conidiophore length would be difficult and unreliable. Neither does division of the genus on the basis of the manner of

conidiophore emergence, as suggested by von Höhnelt, appear to be feasible; for if it is determined by the nature of the host, as suggested by Lindau, rather than by any inherent quality of the fungus, the manner of emergence is hardly suitable or even valid as a basis for a division.

For convenience, morphologic characters may be grouped into two categories, those which are constant and those which are variable. Only those which are fairly constant are of much value. If all the characters of the *Cercospora* species were as variable as the length of the conidia and conidiophores, it would be difficult to divide the genus into groups or to recognize species. However, a comparison of over 100 species has revealed characters which, for the cases examined at least, appear to be fairly constant.

The contrasted characters revealed by the comparisons that appear to have a value as a basis for dividing the genus into sections are: (1) the presence or absence of an external mycelium; (2) conidiophores simple or branched; (3) conidiophores arising from a tuberculate stroma, a loose to fairly compact stroma, or non-stromatic; (4) conidia acicular-obclavate, abruptly obclavate, or cylindrical.

Of these sets of characters, the first two are most significant. The reason for this is that they involve the presence or absence of structural units. These characters are, therefore, used as primary division characters. The presence or absence of an external mycelium is used first. In the cases in which an external mycelium was observed, it was constant for all the specimens examined, and was present in sufficient quantity to make it easy to assign the fungus to a category based on its presence. A little greater difficulty arises with respect to the use of the presence or absence of branched conidiophores since in the transitional groups the branching is limited to a very small percentage of the conidiophores, e.g., *C. beticola* Sacc. In this particular species, only 1.35 per cent of the conidiophores were branched. The question, therefore, arises as to how much branching is necessary in order that a species be grouped in a section characterized by branched conidiophores. Should as fine a distinction be drawn here as has been in regard to setae in *Gloeosporium* and *Colletotrichum*? Such a course appears to be ill-advised. It appears more useful to consider those species branched in which the character is consistently revealed upon careful search, even though the percentage be low. On the other hand, species in which only a single case of branching is observed, or species in which the percentage of branching is very low but does not occur regularly, are not considered as having branched conidiophores and are placed in the sections having simple conidiophores.

There are two types of branching, opposite and irregularly alternate. The former type is found in *C. cercidicola* Ell. (Fig. 5) and the latter in *C. ferruginea* Fckl. (Fig. 6). Both types are combined in *C. illinoensis*

Barth. (Fig. 8). Three groupings are, therefore, possible on the basis of branching.

The other sets of characters—conidiophores arising from a tuberculate stroma, or a loose to fairly compact stroma, or non-stromatic, and conidial shape—involve degrees of expression of single characters, and consequently there is considerable intergradation between the distinct types. They are, therefore, a little more difficult to use. However, in the specimens examined, they appear to be constant for single species, which makes it possible to employ them in a division of the genus.

The nature of the stroma and of the conidial types has been defined in the morphological discussion. Suffice it to state here that two groupings are possible on the basis of the nature of stromatic expression: (1) stroma tuberculate or pseudoparenchymatic and (2) stroma composed of loosely to fairly compactly interwoven hyphae or rarely none produced. While five types of conidia have been defined, only three groupings are possible under this heading. These are groups with species having cylindrical, abruptly obclavate, or acicular-obclavate conidia. The last group includes species with acicular conidia and narrowly obclavate conidia. These two types are not readily separable. Species having these two types of conidia are, therefore, grouped together as acicular-obclavate. In the first group are included species with fusiform conidia.

Using the characters above discussed, the species of the genus so far studied have been grouped into sections as shown in the following systematic arrangement of the genus.

SYSTEMATIC ARRANGEMENT OF THE GENUS

CERCOSPORA Fresenius

Cercospora Fresenius, Beitr., 3:91, 1863.—Frank, Krank. d. Pfl., p. 600, 1880.—Saccardo, Mich., 2:29, 1880; Syll. Fung., 4:431, 1886.—Costantin, Les Mucedineès Simples, p. 77, 1888.—Lindau in Engler and Prantl, Nat. Pflanzenfam., 1:1:486, 1900; and in Rabenhorst's Kryptogamen-Flora, 9:86, 1910.—Massee, Diseases of Cultivated Plants and Trees, p. 483 1910.—Stevens, The Fungi which Cause Plant Disease, p. 625, 1921; Plant Disease Fungi, p. 413, 1925.

Syn. *Virgasporium* Cooke, Grev., 3:182, 1875.

Cercosporella Saccardo, in part, Mich., 2:20, 1880; Syll. Fung., 4:218, 1886.—Costantin, Les Mucedineès Simples, p. 74,, 1888.—Lindau in Engler and Prantl, Nat. Pflanzenfam. 1:1:451, 1900; and in Rabenhorst's Kryptogamen-Flora, 8:421 1910.—Smith and Ramsbottom, Trans. Brit. Myc. Soc., 5:166, 1915.—Stevens, The Fungi which Cause Plant Disease, 592, 1921; Plant Disease Fungi, p. 395, 1925.

Cercosporina Spegazzini, in part, Myc. Arg., 5:424, 1910.—Saccardo, Syll. Fung., 22:1432, 1913.

Mycelium internal or in part external. Conidiophores tufted, emerging through the stomata, rupturing the epidermis, or in part effused on the external mycelium when the latter is present, simple or branched, more or less geniculate, straight or flexuous, continuous or septate, non-stromatic or arising from a loose to tuberculate stroma, hyaline to dark brown. Conidia acrogenous, at times appearing lateral due to the further development of the conidiophores, acicular, narrowly obclavate, abruptly obclavate, fusiform, or cylindrical, filiform, septate, hyaline to dark brown.

The type species is *Cercospora apii* Fresenius.

KEY TO SECTIONS OF CERCOSPORA

- I. Mycelium internal
 - A. Conidiophores simple
 1. Stroma tuberculate
 - a. Conidia acicular-obclavate Section I
 - b. Conidia abruptly obclavate Section II
 - c. Conidia cylindrical Section III
 2. Stroma not tuberculate, composed of loosely to fairly compactly interwoven hyphae, or rarely none produced
 - a. Conidia acicular-obclavate Section IV
 - b. Conidia abruptly obclavate Section V
 - c. Conidia cylindrical or somewhat fusiform Section VI
 - B. Conidiophores branched
 1. Branching opposite, stroma not tuberculate, composed of loosely to fairly compactly interwoven hyphae, or rarely none produced, conidia abruptly obclavate Section VII
 2. Branching alternate
 - a. Stroma tuberculate
 1. Conidia acicular-obclavate Section VIII
 2. Conidia cylindrical Section IX
 - b. Stroma not tuberculate, composed of loosely to fairly compactly interwoven hyphae or rarely none produced, conidia cylindrical Section X
 3. Branching alternate and opposite, stroma composed of loosely to fairly compactly interwoven hyphae, or rarely none produced, conidia cylindrical Section XI
- II. Mycelium internal and external
 - A. Conidiophores simple
 1. Stroma tuberculate
 - a. Conidia acicular-obclavate Section XII
 - b. Conidia abruptly obclavate Section XIII
 - c. Conidia cylindrical Section XIV
 2. Stroma not tuberculate, composed of loosely to fairly compactly interwoven hyphae, or rarely none produced
 - a. Conidia acicular-obclavate Section XV
 - b. Conidia abruptly obclavate Section XVI
 - B. Conidiophores branched
 1. Branching alternate
 - a. Stroma tuberculate, conidia abruptly obclavate Section XVII
 - b. Stroma not tuberculate, composed of loosely to fairly compactly interwoven hyphae, or rarely none produced
 1. Conidia acicular-obclavate Section XVIII
 2. Conidia abruptly obclavate Section XIX
 3. Conidia cylindrical Section XX
 2. Branching alternate and opposite, stroma composed of loosely to fairly compactly interwoven hyphae, or rarely none produced, conidia cylindrical Section XXI

SECTION I

Mycelium internal, conidiophores simple, stroma tuberculate, conidia acicular-obclavate.

Cercospora lysimachiae Ellis and Halsted, Jour. Myc., 6:34, 1890.—Saccardo, Syll. Fung., 10:631, 1892.

Type locality: New Brunswick, N. J., B. D. Halsted, Sept. 1889, Ellis and Everhart, N. Amer. Fungi, Sec. Ser., No. 2475. Collected previously by B. D. Halsted, Jonesburg, N. J., July 1889.

Spots none. Mycelium internal, subhyaline to light greenish-yellow, very fine, $1.5\text{--}2.5\mu$, stromatic mycelium yellowish-brown to dark brown, $3\text{--}7.5\mu$. Conidiophores amphigenous but mostly hypophyllous, densely tufted, the tufts being effused over the leaf surface, emerging through the stomata, simple, or very rarely with short irregular branches, subflexuous to flexuous, spreading, arising from a tuberculate stroma, Sudan brown, $25\text{--}90\times 4\text{--}6\mu$, continuous or 1–4 septate, somewhat irregularly constricted at septa, conidial scars rather indistinct. Conidia narrowly obclavate to acicular, dilute yellowish to yellowish-brown, $35\text{--}175\times 2.5\text{--}4\times 1.5\text{--}2.5\mu$, continuous or obscurely 1–15 septate.

On leaves of **Lysimachia stricta* Ait.

Specimens examined: Ellis and Everhart, N. Amer. Fungi, Sec. Ser., No. 2475 (type) (New Brunswick, N. J.).

Cercospora smilacina Saccardo, Mich., 2:364, 1880; Fungi Ital., Pl. 681, 1881; Syll. Fung., 4:476, 1886.—Lindau, in Rabenhorst's Kryptogamen-Flora, 9:799, 1910.

Type locality: Collioure, France, O. Debeaux.

Spots amphigenous, circular to somewhat angular, more or less vein-limited, at times confluent, 1–4 mm., dark brown, with a slight reddish tint above; border definite, raised, blackish-brown on inner margin, light brown to brown on outer margin, or frequently of the same color as the spots below, $150\text{--}300\mu$, the whole surrounded by a narrow yellowish discolored area. Mycelium internal, irregular, olivaceous to olive-brown, $3\text{--}10\mu$, forming here and there compact stromatic mats. Conidiophores amphigenous, densely to very densely tufted, rupturing the epidermis,

* Starred names indicate hosts on which the fungus has been seen by the writer.

with a bulbous base, simple, straight to subflexuous, arising from a large, compact, tuberculate stroma, Dresden brown, $15-55 \times 4-4.5\mu$, continuous or 1-2 septate, conidial scars distinct, more or less shouldered, scattered. Conidia at first cylindrical, then narrowly obclavate, light olive-brown, $25-100-160 \times 3-4 \times 2-3\mu$, 1-13 septate. [Fig. 10]

On leaves of **Smilax aspera* L.

The above description agrees very well with that of Saccardo with the exception of the size of the conidia. In the Krypt. Exs. specimen No. 728b the conidia agreed very well with the measurements given by Saccardo. Only a few of the longer ones listed above were found. In the same exsiccati, specimen No. 728a, the longer conidia were more abundant than the shorter ones.

This species is closely allied to *C. smilacis* Thüm. but differs from it in the shorter, narrower, and unbranched conidiophores and in the more definitely attenuated conidia. From *C. petersii* (B & C.) Atk. it differs in its much shorter and narrower conidiophores and much narrower conidia. The conidia of the latter taper abruptly, those of *C. smilacina* Sacc. taper gradually.

Saccardo lists *C. smilacis* Peck as a synonym of his species. Peck, however, has no such species. The fungus described by Peck was listed under *C. smilacis* Thüm. and is now referred to *C. petersii* (B. & C.) Atk. (l.c.).

Migula's specimen listed below appears to belong here. The material was such, however, that this could not be determined with absolute certainty.

Specimens examined: Krypt. Exs., Nos. 728a (Abbazia, Litoriale austriacum), and 728b (Lussinpiccola, Lussin Island.)—Migula, Crypt. Ger., Aust. et Helv. Exs., Fasc. 33. Pilze. No. 179 (Abbazia, Istria).

Cercospora gaultheriae Ellis and Everhart, Jour. Myc., 2:2, 1886. On *Gaultheria procumbens* L., Ellis and Everhart, N. Amer. Fungi, Sec. Ser., No. 1514 (Newfield, N. J.).

Cercospora occidentalis Cooke, Hedw., 17:39, 1878. On *Cassia occidentalis* L., Ellis, N. Amer. Fungi, No. 642 (Aikin, S. Car.)

Cercospora ticinensis Briosi and Cavara, I Funghi Parass., No. 336, 1900. On *Sambucus nigra* L., (type) (Pavia, Italy).

Cercospora vernoniae Ellis and Kellerman, Am. Nat., 17:1116, 1883. On *Vernonia baldwinii* Torr., Ellis and Everhart, N. Amer. Fungi, Sec. Ser., No. 3090 (Rockfort, Kan.).

Cercospora zinniae Ellis and Martin, Jour. Myc., 1:20, 1885. On *Zinnia pauciflora* L., Ellis and Everhart, N. Amer. Fungi, Sec. Ser., No. 1507 (type) (Green Cove Springs, Fla.).

Cercospora zonata Winter, Bol. Soc. Brot., 2:49, 1883. On *Vicia faba* L., Rabenhorst-Winter, Fungi Europaei, Ser. II, No. 3294 (Coimbra, Italy).

SECTION II

Mycelium internal, conidiophores simple, stroma tuberculate, conidia abruptly obclavate.

Cercospora desmanthi Ellis and Kellerman, Jour. Myc., 3:14, 1887—Saccardo, Syll. Fung., 10:641, 1892.

Syn. *Cercospora condensata* Ellis and Kellerman, var. *desmanthi* Ellis and Kellerman, Jour. Myc., 1:2, 1885.—Saccardo, Syll. Fung. 4:436, 1886.

Type locality: Great Bend, Kansas, W. A. Kellerman, 1884.

Spots amphigenous, brown to blackish-brown, appearing as minute dark punctiform dots due to the abundance of conidiophores which practically cover the spots. The whole leaflet eventually is killed and turns brown. Mycelium internal, light olivaceous to olive-brown, 2–5 μ , stromatic mycelium of the same color but somewhat coarser, up to 8 μ . Conidiophores amphigenous but mostly hypophyllous, very densely tufted, the tufts closely aggregated and only a few to each spot, rupturing the epidermis, simple, subflexuous to flexuous, arising from a short flattened, somewhat loose to compact, tuberculate stroma, dilute Dresden brown to dilute olive-brown, 35–80 \times 3.5–5.6 μ , 1–4 septate towards bases or in region below the surface of the host, conidial scars distinct, more or less shouldered. Conidia abruptly obclavate, light yellowish-olive to buffy olive, 15–40 \times 5.6–6.4 \times 2.5–4 μ , continuous or 1–3 septate.

On leaves of **Desmanthus illinoensis* (Michx.) MacM.

Specimens examined: Ellis and Everhart, N. Amer. Fungi, Sec. Ser., No. 1992 (Manhattan, Kan.).

Cercospora fraxini (DeCandolle) Saccardo, Syll. Fung., 4:471, 1886. On *Fraxinus excelsior* L., Roumeguère, Fungi Sel. Gallici Exs., No. 5692. (Noidan, Côte-d'Or, France).

Cercospora personata (Berkely and Curtis) Ellis, Jour. Myc., 1:63, 1885. On *Arachis hypogaea* L., Ellis and Everhart, N. Amer. Fungi, Sec., No. 2480 (Starkville, Miss.).

Cercospora viticola (Cesati) Saccardo, Syll. Fung., 4:458, 1886. On *Vitis* sp., Briosi and Cavara, I Funghi Parass., No. 114 (Tenn.)

SECTION III

Mycelium internal, conidiophores simple, stroma tuberculate, conidia cylindrical.

Cercospora bupleuri Passerini, in Thümen, Myc. Univ., No. 1375. 1879.—Saccardo, Syll. Fung., 4:442, 1886.—v. Höhnelt, Ann. Myc., 1:530, 1903.—Lindau, in Rabenhorst's Kryptogamen-Flora, 9:126, 1910,

Type locality: Parma, Vigheffio, Italy, Passerini, Sept. 1878, Thümen, Myc. Univ., No. 1375.

Spots amphigenous and caulicolous, circular to elliptical, 1.5×0.5 –2 mm., reddish-brown on stems, becoming yellowish to white centered, on leaves reddish-brown to dirty-brown, becoming light centered; border definite, dark brown. Mycelium internal, subhyaline, 2.5 – 4.5μ , stromatic mycelium yellowish-brown to olive-brown, 2.5 – 6.5μ . Conidiophores amphigenous and caulicolous, moderately to densely tufted, rupturing the epidermis, simple, flexuous, arising from a somewhat loose to compact tuberculate stroma, dilute brownish-olive, 15 – 45×2.5 – 4.5μ , at times much inflated at bases, up to 7.5μ , continuous or 1–2 septate at bases; conidial scars minute but distinct, shouldered, scattered. Conidia oblong-cylindrical to bacilliform, tapering very slightly, straight or somewhat curved, subhyaline to light yellowish, 20 – 65×2 – 3.5×2 – 3μ , continuous or 1–3–5 septate.

On leaves and stems of **Bupleurum tenuissimum* L.

Specimens examined: Thümen, Myc. Univ., No. 1375 (type) (Vigheffio, Parma, Italy).

Cercospora tuberosa Ellis and Kellerman, Bull. Tor. Bot. Club, 11:116, 1884.—Ellis and Everhart, Jour. Myc., 1:38, 1885.—Saccardo, Syll. Fung., 4:439, 1886.

Syn. *Cercospora glaucescens* Winter, Rabenhorst-Winter, Fungi Europaei, Ser. II, No. 3080, 1884; Hedw., 23:171, 1884.

Spots amphigenous, irregular, often confluent, vein-limited, 0.5–3 mm., at first dark brown above and glaucescent below, becoming light rusty-brown to whitish; border indefinite. Mycelium internal, subhyaline to olivaceous to olive-brown, 1.5 – 6μ , stromatic mycelium olive-brown, 3 – 9μ . Conidiophores hypophyllous, rarely epiphyllous, moderately to densely tufted, emerging through the stomata, simple, straight to subflexuous, arising from a large tuberculate stroma, olive-brown, 35 – 80×3 – 5μ , 1–5 septate, conidial scars indistinct. Conidia oblong-cylindrical, slightly attenuated towards apices, yellowish to pale olivaceous, 35 – 140 – 190×3.5 – 5×3 – 4μ , 3–15–20 septate, slightly or not at all constricted at septa. [Fig. 12.]

On leaves of **Apios tuberosa* Moench.

Specimens examined: As *C. tuberosa* Ell. and Kell., Bartholomew, Fungi Columb., No. 2614 (Wood River, Neb.). As *C. glaucescens* Wint.

Rabenhorst-Winter, Fungi Europaei, Ser. II, No. 3080 (Perryville, Mo.).

Cercospora destructiva Ravenel, Jour. Myc., 3:13, 1887. On *Euonymus japonicus* L., Ellis and Everhart, N. Amer. Fungi, Sec. Ser., No. 1760 (Aiken, S. Car.).

Cercospora hyppophylla Cavara, Rev. Myc., 21:103, 1899. Pl. CXCVII, figs. 9, 10. On *Rosa canina* L., Briosi and Cavara, I Funghi Parass., No. 335 (Vallombrosa, Italy).

Cercospora platanicola Ellis and Everhart, Jour. Myc., 3:17, 1887. On *Platanus occidentalis* L., Ellis and Everhart, N. Amer. Fungi, Sec. Ser., No. 1766 (Point a la Hache, La.).

Cercospora protearum Cooke, Grev., 12:39, 1883. On *Leucospermum conocarpum* R. Br., Rabenhorst-Winter, Fungi Europaei, Ser. II, No. 3589 (Bonae Spei, Hottentot, Holland).

SECTION IV

Mycelium internal, conidiophores simple, stroma composed of loosely to fairly compactly interwoven hyphae, or rarely none produced, conidia acicular-obclavate.

Cercospora acalyphae Peck, 34 Rep. N. Y. State Mus., p. 48, 1881.—Ellis and Everhart, Jour. Myc., 1:20, 1885.—Saccardo, Syll. Fung., 4:457, 1885.—Atkinson, Jour. Eli. Mitch. Sci. Soc., 8:46, 1891.—Carver, Proc. Ia. Acad. Sci., 8:162, 1900.—Davis, Trans. Wis. Acad., 14:95, 1903.—Schwarze, N. J. Ag. Exp. Sta. Bull., 313:128, 1917. figs. 771-772.

Type locality: Albany, New York.

Spots amphigenous, circular to somewhat irregular, rarely confluent, small, about 0.3-3 mm., at first brown, then brownish-white to grayish-white above, brown, light-brown, to grayish-brown below; border definite, slightly raised, dark-brown to purplish-brown, 110-250 μ , the whole at times surrounded by a narrow, yellow translucent area. Mycelium internal, regular to sub-irregular, much branched, hyaline to subhyaline, 1.5-3 μ . Conidiophores amphigenous, mostly epiphyllous, frequently absent from the lower surface of the spots, loosely tufted, rupturing the epidermis or emerging through the stomata, simple, straight to subflexuous, non-stromatic to stromatic, Brussels brown to olive-brown, the color much diluted towards the apices, 20-200 \times 3.5-5 μ , continuous to 1-3 septate, conidial scars distinct, aggregated towards the tips or scattered. Conidia acicular, hyaline, subhyaline to yellowish-green, 35-200 \times 2-3 \times 1.5-2 μ , 2-15 closely septate. [Fig. 2.]

On leaves of *Acalypha virginica* L., *A. gracilens* Gray, and leaves and stems of *A. ostryaefolia* Riddell.

Specimens examined: Ellis and Everhart, N. Amer. Fungi, Sec. Ser., No. 1523 (Manhattan, Kan.); Fungi Columb., No. 694 (Nuttallburg, W.

Va.).—Seymour and Earle, Ec. Fungi, No. 382 (Millstone, N. J.).—Herb. Univ. of Ill. ex Herb. of F. L. Stevens, specimen collected at New Brunswick, N. J., Aug. 6, 1892.

Cercospora acnidae Ellis and Everhart, Proc. Acad. Nat. Sci. Phil., 1891, p. 89.—Saccardo, Syll. Fung., 10: 637, 1892.

Type locality: Wilmington, Del., A. Commons, No. 1011, Sept. 1889. Prototype, Ellis and Everhart, N. Amer. Fungi, Sec. Ser., No 2582, Wilmington, Del., A. Commons, Sept. 1890.

Spots amphigenous, circular to somewhat angular, more or less vein-limited, 1–3 mm., brownish to dirty white; border definite, raised, dark brown, 150–500 μ . Mycelium internal, hyaline to dilute yellowish-brown, 2–7.5 μ . Conidiophores amphigenous, loosely to fairly densely tufted, rupturing the epidermis, simple, straight to subflexuous, arising from a loose to fairly compact stroma, olivaceous to Dresden brown, 25–75 \times 3.5–5.5 μ , continuous or 1 septate, conidial scars fairly distinct. Conidia narrowly obclavate, hyaline to light greenish-yellow, 20–75 \times 3–4 \times 1.5–2.5 μ , 1–10 septate.

On leaves of **Acnida cannabina* L.

Specimens examined: Ellis and Everhart, N. Amer. Fungi, Sec. Ser., No. 2582 (prototype) (Wilmington, Del.).

Cercospora ageratoides Ellis and Everhart, Jour. Myc. 5: 71, 1889.—Saccardo, Syll. Fung., 10: 627, 1892.—Tracy and Earle, Miss. Agric. Exp. Sta. Bull., 34: 116, 1895.—Schwarze, N. J. Agric. Exp. Sta. Bull., 313: 128, 1927. fig. 773.—Davis, Trans. Wis. Acad., 19: 2: 675, 1919.

Type locality: Newfield, N. J., July to September 1885.

Spots indefinite, the tufts of conidiophores forming more or less vein-limited, olivaceous to Brussels brown, velvety patches on both surfaces of the leaves but especially on the lower surface. Mycelium internal, hyaline, 1–2.5 μ ; stromatic mycelium 2–6 μ . Conidiophores amphigenous, loosely to moderately tufted, emerging through the stomata, subflexuous, subundulate, simple, or rarely irregularly branched, arising from a small, fairly compact stroma, Brussels brown to Argus brown, 20–90 \times 4.5–5 μ , 1–5 irregularly septate, at times somewhat constricted at septa, conidial scars fairly distinct, more or less warty, rarely shouldered. Conidia cylindrical to narrowly obclavate, yellowish-olive, 30–160 \times 3–4.5 \times 1.5–2.5 μ , 1–13 septate.

On leaves of *Eupatorium urticaefolium* L., **E. album* L., and *E. rotundifolium* L.

Specimens examined: Ellis and Everhart, N. Amer. Fungi, Sec. Ser. No. 2473 (Newfield, N. J.).

Cercospora alismatis Ellis and Holway, Jour. Myc., 1: 63, 1885.—Saccardo, Syll. Fung., 4: 478, 1886.

Type locality: Decorah, Iowa, E. W. D. Holway, July.

Spots amphigenous, subcircular to irregular, somewhat confluent, more or less vein-limited, margin undulate, 4–10 mm., dirty brown above, olive-brown below, becoming grayish centered; border indefinite. Mycelium internal, almost regular or irregular, subhyaline to very dilute Dresden brown, $2\text{--}7.5\mu$, stromatic mycelium Dresden brown, somewhat penicillioidly branched. Conidiophores amphigenous, loosely to moderately tufted, emerging through the stomata, simple or very rarely irregularly branched, straight or flexuous, arising from a loose to compact stroma, Dresden brown, $40\text{--}250 \times 4.5\text{--}6\mu$, 1–7 septate, conidial scars distinct, scattered, shouldered or laterally displaced. Conidia narrowly obclavate, subhyaline to light greenish-yellow, $50\text{--}180\text{--}265 \times 3\text{--}5 \times 1.5\text{--}3\mu$, 4–10–21 septate.

On leaves of **Alisma plantago-aquatica* L.

Specimens examined: Ellis and Everhart, N. Amer. Fungi, Sec. Ser., No. 3191; Fungi Columb., No. 597.—Herb. Univ. of Ill. ex Crypt. Herb. of F. L. Stevens, No. 80 (All from Cicero, N. Y.).

Cercospora alternantherae Ellis and Langlois, Jour. Myc., 6: 36, 1890.—Stevens, Trans. Ill. Acad. Sci., 10: 211, 1917.

Type locality: St. Martinsville, Louisiana, Langlois, No. 1430.

Spots amphigenous, circular, rarely confluent, more or less convex above and concave below, dull-brown to olive-brown, becoming grayish to whitish centered, 0.5–2 mm. in diameter; border definite, raised, brown to dark-brown, $75\text{--}225\mu$, the whole surrounded by a narrow brownish to yellow translucent area. Mycelium internal, irregular, adjacent cells frequently of different size, subhyaline to light brownish-yellow, $1\text{--}3\mu$. Conidiophores amphigenous, solitary to loosely tufted, the tufts scattered over the spots, emerging through the stomata or rupturing the epidermis, simple, straight to flexuous, borne on a short, loose to compact stroma, or, especially when solitary, non-stromatic, amber-brown to Brussels brown, $40\text{--}285 \times 3\text{--}4\mu$, continuous to distantly 1–6 septate, conidial scars distinct and scattered. Conidia acicular, at times narrowly obclavate to slightly fusiform, hyaline to subhyaline, $55\text{--}230 \times 2\text{--}2.5 \times 1\text{--}1.5\mu$, continuous to obscurely several septate.

On leaves of *Alternanthera achyrantha* R. Br. and **A. portoricensis* Kuntze. The fungus on *A. portoricensis* differs somewhat from the original description of *C. alternantherae* Ell. & Langl. on *A. achyrantha* in conidiophore and conidial measurements and septation. The original description with respect to these characters is as follows: "hyphae, $25\text{--}30 \times 5\mu$, continuous . . . ; conidia . . . 1–3 septate, $65\text{--}80 \times 3\mu$." These characters for the fungus on *A. portoricensis* are: conidiophores $40\text{--}285 \times 3\text{--}4\mu$, continuous to 1–6 septate; conidia $55\text{--}230 \times 2\text{--}2.5\mu$, continuous to obscurely several septate. A comparison of the two indicates that either

the original description was based on young material or that the two are distinct. The latter contention, however, is not borne out by a comparison of the spots produced, the manner of conidiophore production, nor conidiophore and conidial shape and color. The fungi on the two host species are, therefore, in all probability members of the same species.

Specimens examined: Herb. Univ. of Ill. Porto Rican Fungi, Nos. 3976 and 8479 (Coama, Porto Rico).

Cercospora apii Fresenius, Beitr., 3:91, 1863. Pl. XI, figs. 46-54.—Frank, Krank. d. Pflanzen, p. 603, 1880.—Ellis and Everhart, Jour. Myc. 1: 36, 1885.—Saccardo, Syll. Fung., 4: 442, 1886; Fungi Ital., Pl. 667.—Scribner, Rep. Sec. Agric., U. S., 1886, p. 117. Pl. V.—Atkinson, Cornell Bull., 49: 314, 1892. fig. 5.—Briosi and Cavara, I Funghi Parass., Fasc. XI, No. 268, 1896. figs. 1-3.—Duggar and Bailey, Cornell Bull., 132: 201, 1897. figs. 48-50.—Prillieux, Malad. d. Plant. Agric., 2: 355, 1897. fig. 406.—Hume, Fla. Sta. Rept. 1899 and 1900, p. 34. Pl. II.—Kirchner, Krank. u. Beschäd. unser land. Kulturpfl., 2nd Ed., pp. 296, 355, 1906.—Kirchner and Boltshauser, Atlas III, Pl. 10, figs. 1-2.—Lindau in Rabenhorst's Kryptogamen-Flora, 9: 123, 1910.—Massee, Diseases Cult. Plants, p. 486, 1910. fig. 147.—Schwarze, N. J. Bull., 313: 130, 1917, figs. 780-781.—Stevens, Fungi Which Cause Plant Disease, p. 628, 1921. fig. 426.—Klotz, Mich. Sta. Tech. Bull., 63, 1923. Pls. I-IX.—Stevens, Plant Disease Fungi, p. 414, 1925. fig. 388.

Type locality: Germany (?)

Spots amphigenous, subcircular to somewhat angular, more or less confluent, at times vein-limited, frequently causing contortion of the leaf, 1-10 mm. to 2 cm., at first dark green, becoming yellowish towards the centers, then pale brown to tan, and eventually whitish, not infrequently appearing olivaceous due to the abundance of conidiophores; border indefinite to definite, not raised or slightly raised, olivaceous, about 60μ wide. Mycelium internal, irregular, hyaline, subhyaline, light yellowish-brown to olivaceous, $1.5-3.5\mu$, $3.5-6.5\mu$ in the stromata. Conidiophores amphigenous, solitary to rather densely tufted, rupturing the epidermis or emerging through the stomata, simple or rarely branched, straight to flexuous, with a more or less bulbous base, arising from a stroma formed from loosely to fairly compactly interwoven hyphae, yellowish-brown to olive-brown, $20-125 \times 3-6\mu$, continuous to 1-2 septate towards bases, conidial scars distinct, aggregated towards the tips or somewhat scattered. Conidia at first more or less cylindrical, then somewhat fusiform, and finally acicular to acicular-obclavate, subhyaline to light yellowish-green, $15-195 \times 2.5-4.5 \times 1-3\mu$, continuous to 1-25 closely septate. [Fig. 1.]

On leaves and stems of **Apium graveolens* L. and *A. graveolens* L. var. *rapaceum* DC.

Klotz lists conidiophores up to 180μ and not infrequently having cross walls throughout their whole length. He also lists conidia to 290μ with 29 cross walls.

Considerable variability exists in conidiophore and conidial measurements of several of the specimens examined. Some of these measurements are as follows: conidiophores $25-125 \times 3.3-4.5\mu$, conidia $20-175 \times 2.5-3.8 \times 1.3-2.5\mu$; conidiophores $20-75 \times 4.5-5.8\mu$, conidia $28-195 \times 3-4.2 \times 2-3\mu$; conidiophores $20-80 \times 4-6\mu$, conidia $15-160 \times 3-4 \times 1.5-3\mu$; conidiophores $20-55 \times 3.5-4.5\mu$, conidia $20-150 \times 2.5-4 \times 1-2.2\mu$. The septation of the conidia in these cases varied directly with their length. The above differences may mean that *Cercospora apii* consists of several varieties. It is more probable, however, that the variations are due to external environmental factors than to internal factors, since size alone is the apparent variable.

Specimens examined: v. Thümen, Herb. Myc. Oec., No. 463 (Conegliana, Italy).—Briosi and Cavara, I Funghi Parass., No. 268 (Meaux, France).—Roumeguère, Fungi Sel. Exs., No. 6906 (Meaux, France).—Ellis and Everhart, N. Amer. Fungi, Sec. Ser., No. 1739a (Columbia, Mo.); Fungi Columb., No. 885a (London, Canada).—Seymour and Earle, Ec. Fungi, Nos. 440a (Columbus, Ohio) and 440b (New Brunswick, N. J.).—Bartholomew, Fungi Columb., No. 4004 (St. Paul, Neb.).

Cercospora atrogrisea Ellis and Everhart, Proc. Acad. Nat. Sci. Phila., 1893, p. 464.—Saccardo, Syll. Fung., 11: 625, 1896.

Type locality: Newfield, N. J., Ellis and Everhart, N. Amer. Fungi, Sec. Ser., No. 3089; Fungi Columb., No. 394.

Spots none, the conidia and conidiophores forming gray to slaty-black patches on pods and stems. Conidiophores densely tufted, the tufts closely compacted, seated on a vertically elongated, compact stroma, simple, with a bulbous base, straight to subflexuous, cinnamon brown, $40-110 \times 4-5\mu$, continuous to 1-6 septate, conidial scars distinct and rather distantly scattered. Conidia acicular, rarely narrowly obclavate, subhyaline, $50-200 \times 3-4 \times 1.5-2\mu$, 6-18 closely septate.

On dead stems and pods of **Raphanus sativus* L.

Specimens examined: Ellis and Everhart, N. Amer. Fungi, Sec. Ser., No. 3089 (type) (Newfield, N. J.); Fungi Columb., No. 394 (type) (Newfield, N. J.).

Cercospora davisii Ellis and Everhart, Proc. Acad. Nat. Sci. Phil., p. 89, 1891.—Atkinson, Jour. Elishu Mitch. Sci. Soc., 8: 60, 1891.—Saccardo, Syll. Fung., 10: 622, 1892.—Davis, Trans. Wis. Acad., 21: 275, 1924.

Type locality: Racine, Wisconsin, J. J. Davis, No. 1089. Topo-type: J. J. Davis, Racine, Wis., 1890. Issued in Ellis and Everhart, N. Amer. Fungi, Sec. Ser., No. 2581.

Spots amphigenous, subcircular, more or less vein-limited, at times confluent, 1–5 mm., greenish to dark brown; border indefinite or in part definite, slightly raised, yellowish-brown, $30\text{--}75\mu$ wide. Mycelium internal, hyaline, subhyaline to light brownish-yellow, $1.5\text{--}4.5\mu$. Conidiophores amphigenous, loosely to somewhat densely tufted, emerging through the stomata or rupturing the epidermis, simple, straight to subflexuous, with or without a bulbous base, arising from a stroma of loosely to fairly compactly interwoven, irregular hyphae, pale Dresden brown, $20\text{--}85\times 3\text{--}6\mu$, continuous or 1–2 septate above the bases, conidial scars distinct, shouldered mostly aggregated towards the tips. Conidia at first cylindrical, then acicular, subhyaline to light greenish-yellow, $20\text{--}140\times 2.2\text{--}4.5\times 1.2\text{--}2.5\mu$, at first continuous, becoming closely 1–13 septate.

On leaves and stems of **Melilotus alba* Desr.

Davis records conidiophores up to 140μ .

Specimens examined: Ellis and Everhart, N. Amer. Fungi, Sec. Ser., No. 2581 (Racine, Wis.).—Bartholomew, Fungi Columb. No. 1811 (Stockton, Kans.).

Cercospora demetrioniana Winter, Hedw., 23: 170, 1884; Rabenhorst-Winter, Fungi Europaei, Ser. II, No. 3079, 1886.—Ellis and Everhart, Jour. Myc., 1: 34, 1885.—Saccardo, Syll. Fung., 4: 439, 1886.

Spots amphigenous, circular, at times confluent, mostly concentrically zoned, rusty-brown to dark-brown above, light-brown to deep olive-brown below, not very definitely limited, 1–1.5 mm. in diameter. Mycelium internal, regular to irregular, mostly fine, subhyaline to greenish-yellow, becoming quite coarse near stromatic areas, the coarser mycelium being yellow to yellowish-brown, $1.5\text{--}6\mu$ in diameter. Conidiophores amphigenous, solitary to somewhat densely tufted, tufts scattered, rupturing the epidermis or emerging through the stomata, arising from a loose to fairly compact stroma, simple, straight to subflexuous, Brussels-brown, $40\text{--}350\times 4\text{--}6\mu$, 1–10, remotely septate, conidial scars distinct and distantly scattered. Conidia acicular to somewhat fusiform, rarely narrowly obclavate, hyaline to greenish-yellow, $50\text{--}210\times 3.5\text{--}5.5\times 1.5\text{--}3\mu$, 7–16 very closely septate.

On leaves of **Crotalaria sagittalis* L.

The original description lists conidiophores up to 1 mm. in length.

Specimens examined: Rabenhorst-Winter, Fungi Europaei, Ser. II, No. 3079 (type) (Perryville, Mo.).—Ellis and Everhart, N. Amer. Fungi, Sec. Ser., No. 1744 (Faulkland, Del.).

Cerospora echinocystis Ellis and Martin, Am. Nat., 16: 1003, 1882.—Ellis and Everhart, Jour. Myc., 1: 40, 1885.—Saccardo, Syll. Fung., 4: 452, 1886.—Davis, Trans. Wis. Acad., 18: 268, 1916.

Type locality: Lexington, Ky., W. A. Kellerman.

Spots amphigenous, angular, vein-limited, more or less confluent, 0.5–3 mm., light brown, becoming brownish-white to white; border indefinite. Mycelium internal, hyaline, $1.5\text{--}6\mu$, the larger dimensions obtaining just beneath the conidiophores. Conidiophores amphigenous, solitary or loosely tufted, rupturing the epidermis or rarely emerging through the stomata, simple, flexuous, non-stromatic, or rarely with a loose stroma, Dresden brown to Saccardo's umber, $25\text{--}200 \times 3.5\text{--}6\mu$, continuous or 1–5 septate, conidial scars distinct, shouldered, scattered. Conidia acicular to to acicular-obclavate, hyaline to light greenish-yellow, $25\text{--}200 \times 2\text{--}4.5 \times 1\text{--}3\mu$, closely, or rather distantly 1–15 septate.

On leaves of **Echinocystis lobata* (Michx.) T. and G. and **Sicyos angulatus* L.

The above description differs considerably from the original in the measurements given. The maximum length for the conidia and especially for the conidiophores of the original description is much below that given above. However, specimens were examined in which the conidiophores varied from the short ones (45μ) recorded by Ellis and Martin and the longer ones recorded above. No other differences were noted. The variability in length is apparently due to differences in age of the specimens when collected.

In the specimen on *Sicyos angulatus*, Seymour and Earle, Ec. Fungi, No. 285, the conidiophores were not infrequently branched. In other specimens on the same host branching was rare. No branching was observed, on the other host species. The branches were for the most part opposite, subtending a terminal conidial scar. In the branched specimens the geniculations were much more pronounced than in the other. No further significant differences were observed.

For the present the two forms are left under *C. echinocystis* Ell. and Mart., although it is quite possible that they are distinct.

Specimens examined: Ellis and Everhart, N. Amer. Fungi, Sec. Ser., No. 1746 (West Chester, Pa.).—Seymour and Earle, Ec. Fungi, No. 285 (New Brunswick, N. J.).—Herb. Univ. Ill. ex Herb. Univ. Wis., J. J. Davis, Lynxville, Wis., Sept. 9, 1915; Herb. Univ. Ill. ex Crypt. Herb. of F. L. Stevens, New Brunswick, N. J., Aug. 24, 1892.

Cercospora ipomoeae Winter, Rabenhorst-Winter, Fungi Europaei, Ser. II, No. 3585, 1886; Hedw., 26: 34, 1887.—Ellis and Everhart, Jour. Myc., 4: 7, 1888.—Saccardo, Syll. Fung., 10: 633, 1892.—Hennings, Engler's Bot. Jahrb., 34: 605, 1905.—Anderson, U. S. Dept. Ag. Bull., 1366: 54, 1926.

Type locality: Perryville, Mo., Rabenhorst-Winter, Fungi Europaei, Ser. II, No. 3585.

Spots amphigenous, subcircular to angular, somewhat vein-limited, more

or less confluent, 1-4 mm., olivaceous, olive-brown to brown, becoming grayish centered, darker above than below; border definite, raised, blackish-brown, $75-225\mu$, the whole surrounded by a narrow yellow translucent or purplish opaque area. Mycelium internal, more or less irregularly inflated, hyaline to dilute brownish, $1.5-6\mu$. Conidiophores amphigenous, loosely tufted, rupturing the epidermis, simple, straight to flexuous, non-stromatic, or approaching a very loose stromatic condition, dilute Brussels brown, $20-325 \times 3-6\mu$, continuous or 1-7 septate; conidial scars distinct, scattered, more or less shouldered. Conidia acicular, hyaline, $25-330 \times 2.5-3.5 \times 1-2\mu$, somewhat obscurely 1-30 septate.

On leaves of **Ipomoea lacunosa* L., *I. pandurata* G. F. W. Mey, *I. purpurea*. Lam., *I. (Pharbitis) hederacea* Jacq.

In Roumeguère, Fungi Sel. Exs., No. 4487, the host is recorded as *I. laciniosa* L. This, no doubt, should be *I. lacunosa* L., since the former name does not appear in any of the standard indexes.

Specimens examined: Rabenhorst-Winter, Fungi Europaei, Ser. II. No. 3585 (type) (Perryville, Mo.).—Roumeguère, Fungi Sel. Exs., No. 4487 (Concordia, Mo.).

Cercospora lippiae Ellis and Everhart, Jour. Myc., 3: 20, 1887.—Saccardo, Syll. Fung., 10: 632, 1892.—Davis, Trans. Wis. Acad., 14: 96, 1903.

Type locality: Louisiana, Langlois, No. 826.

Spot amphigenous, circular, rarely confluent, brown, dark-brown to grayish-brown above, light-brown, olive-brown to grayish-brown below, 1-3 mm. in diameter; border definite, raised, brown to dark-brown, at times reddish-brown, $150-300\mu$, the whole not infrequently surrounded by a narrow brown to red discolored area. Mycelium internal, almost regular to irregular, hyaline to light yellowish-brown, $1.5-4.5\mu$. Conidiophores amphigenous, densely tufted, emerging through the stomata, simple, straight to subflexuous, arising from a short compact stroma, pale yellowish-brown to olive-brown, $20-55 \times 2.5-4.5\mu$, continuous to 1-2 septate, conidial scars minute but distinct, somewhat warty and closely aggregated. Conidia narrowly obclavate to somewhat fusiform, rarely acicular, subhyaline to light greenish-yellow, $25-350 \times 2-3 \times 1-2\mu$, closely 3-16 septate.

On leaves of **Lippia nodiflora* Michx. and **L. lanceolata* Michx.

Specimens examined: Ellis and Everhart, N. Amer. Fungi, Sec. Ser., No. 3088 (Port Byron, Ill.); Fungi Columb., No. 387 (Port Byron, Ill.).—Bartholomew, Fungi Columb., Nos. 2213 (Belvue, Kans.) and 3005 (Stillings, Mo.).

Cercospora angulata Winter, Hedw., 24: 202, 1885. On *Philadelphus coronarius* L., Rabenhorst-Winter, Fungi Europaei, Ser. II. No. 3588 (type) (Perryville, Mo.).

Cercospora arctii Stevens, Bull. Bernice P. Bishop Mus., 19: 154, 1925.

On *Arctium lappa* L., Herb. Univ. of Ill., Hawaiian Fungi, No. 1096 (Kukuikaele, Hawaii).

Cercospora beticola Saccardo, Fungi Ven., Ser. V, p. 189. 1878. On *Beta vulgaris* L. Various miscellaneous specimens of the Herb. Univ. of Ill.

Cercospora canescens Ellis and Martin, Am. Nat., 16: 1003, 1882. On *Phaseolus lunatus* L., Rabenhorst-Winter, Fungi Europaei, Ser. II, No. 3788 (Perryville, Mo.).

Cercospora clavata (Gerard) Peck, 34 Rept. N. Y. State Mus., p. 48, 1881. On *Asclepias incarnata* L., Herb. Univ. of Ill., No. 32961 *ex* Herb. U. S. Dept. Agric., Div. V. P. P., No. 1131 (Urmeyville, Ind.).

Cercospora cruenta Saccardo, Mich., 2: 140, 1880. On *Phaseolus* sp., Ellis and Everhart, N. Amer. Fungi, Sec. Ser., No. 2294 (Locality not given),

Cercospora depazeoides (Desmazieres) Saccardo, Novo Goirn. Bot. Ital. 8: 187, 1876. On *Sambucus nigra* L., Ellis and Everhart, N. Amer. Fungi, Sec. Ser., No. 1749b (Ames, Ia.).

Cercospora malvarum Saccardo, Mich., 2: 365, 1880. On *Malva rotundifolia* L., Ellis and Everhart, Fungi Columb., No. 884. (Newfield, N. J.).

Cercospora microsora Saccardo, Mich., 2: 128, 1880. On *Tilia europaea* L., Briosi and Cavara, I Funghi Parass., No. 44 (Italy).

Cercospora oculata Ellis and Kellerman, Bull. Torr. Bot. Club, 11: 116, 1884. On *Vernonia baldwinii* Torr., Ellis and Everhart, Fungi Columb., No. 598 (Rockport, Kan.).

Cercospora physalidis Ellis, Am. Nat., 16: 810, 1882. On *Physalis virginiana* Mill., Ellis and Everhart, Fungi Columb., No. 1085 (Rooks Co., Kan.).

Cercospora radiata Fuckel, Symb. Myc., p. 354, 1869. On *Trigonella foenumgraceum* L., Thümen, Myc. Univ., No. 584 (Vigheffio, Parma, Italy).

Cercospora resedae Fuckel, Symb. Myc., p. 353, 1869. On *Reseda odorata* L., Briosi and Cavara, I Funghi Parass., No. 83 (Pavia, Italy).

Cercospora sagittariae Ellis and Kellerman, Jour. Myc., 2: 1, 1886. On *Sagittaria latifolia* Willd., Ellis and Everhart, Fungi Columb., No. 693 (West Townshend, Vt.). [Fig. 7.]

Cercospora squalidula Peck, 33 Rept. N. Y. State Mus., p. 29, 1880. On *Clematis virginiana* L., Rabenhorst-Winter, Fungi Europaei, Ser. II, No. 3288 (Decorah, Ia.).

Cercospora teucrii Ellis and Kellerman, Bull. Torr. Bot. Club, 11: 116, 1884. On *Teucrium canadense* L., Ellis and Everhart, Fungi Columb., No. 459 (Rockport, Kan.).

Cercospora violae-tricoloris Briosi and Cavara, I Funghi Parass., No. 185. On *Viola tricolor* L., (type) (Pavia, Italy).

SECTION V

Mycelium internal, conidiophores simple, stroma composed of loosely to fairly compactly interwoven hyphae, or rarely none produced, conidia abruptly obclavate.

Cercospora magnoliae Ellis and Harkness, Bull. Tor. Bot. Club, 8: 27, 1881.—Ellis and Everhart, Jour. Myc., 1: 35, 1885.—Saccardo, Syll Fung., 4: 459, 1886.—Schwarze, N. J. Bull., 313: 136, 1917, figs. 814-815.

Type locality: Newfield, N. J., Ellis and Harkness, Nov. 1880, Ellis, N. Amer. Fungi, No. 643.

Spots amphigenous, subcircular, more or less vein-limited, minute, 0.3-0.6 mm., dark-brown above, becoming white centered, purplish below; border definite above, raised, dark-brown to brown, 90-150 μ ; below indistinct and not much different from the main spot. Mycelium internal, hyaline to yellowish, 0.5-3 μ , stromatic mycelium brownish-yellow. Conidiophores hypophyllous, densely tufted, rupturing the epidermis, simple, straight to subflexuous, arising from a small stroma, Dresden brown to olive-brown, 25-275 \times 2-3 μ , continuous or several septate, conidial scars more or less indistinct, somewhat warty. Conidia obclavate, straight or curved, more or less constricted at septa, apical cell beak-like, olivaceous, 25-42 \times 5-6 \times 2.5-3.5 μ , 1-3-6 septate.

On leaves of **Magnolia glauca* L.

Specimens examined: Ellis, N. Amer. Fungi, No. 643 (type) (Newfield, N. J.).—Rabenhorst-Winter, Fungi Europaei, Ser. II, No. 3286 (Newfield, N. J.).

Cercospora petroselini Saccardo, Ann. Myc., 10: 321, 1912; Syll. Fung., 22: 1423, 1913.—Ellis and Everhart, Jour. Myc., 1: 37, 1885, sub *Cercospora apii* Fresenius.

Syn. *Cercospora apii* Fresenius var. *petroselini* Saccardo, Syll. Fung., 4: 442, 1886.—Lindau in Rabenhorst's Kryptogamen-Flora, 9: 124, 1910.

Type locality:?

Spots amphigenous, subcircular to circular, more or less vein-limited, 0.5-1.5 mm., greenish to yellowish-brown, appearing olivaceous to black due to abundance of conidiophores; border indefinite. Mycelium internal, irregular, hyaline to light yellowish-brown, 2.2-6 μ , stromatic mycelium Dresden brown to olive-brown, 6-10 μ , the cells of the latter being almost isodimetric. Conidiophores amphigenous, very densely tufted, rupturing the epidermis or emerging through the stomata, inflated upon emerging

from the host, simple, flexuous, distorted, arising from a stroma of closely compacted hyphae, Dresden brown to olive-brown, very dilute towards the tips, $35-85 \times 5-7 \mu$, continuous or 1 septate near the bases; conidial scars distinct, scattered, somewhat warty. Conidia obclavate to cylindrical, hyaline to light greenish-yellow, $15-40 \times 3.5-6 \times 3-3.5 \mu$, 1 septate.

On leaves of **Petroselinum hortense* Hoffm.

Ellis and Everhart describe the conidia as being 1-3 septate and $30-50 \times 5-7 \mu$. Saccardo records them as 1-2 septate and $36-40 \times 4-5 \mu$. In the specimens listed below no conidia were found with more than 1 septum.

Specimens examined: Thümen, Myc. Univ., No. 483 (Parma, Italy); Herb. Myc. Oec., No. 464 (Parma, Italy).

Cercospora superflua Ellis and Holway, Jour. Myc., 2: 2, 1886.—Saccardo, Syll. Fung., 4: 471, 1886.

Type locality: Decorah, Iowa, E. W. D. Holway, Aug. 1885, Ellis and Everhart, N. Amer. Fungi, Sec. Ser., No. 1525.

Spots amphigenous, subcircular to irregular, more or less vein-limited, 2-7 mm., light brown; border definite, very slightly raised, a little darker brown than the spot, 50-100 μ . Mycelium internal, hyaline, 1.5-4.5 μ , stromatic mycelium 3-7.5 μ . Conidiophores amphigenous, moderately to somewhat densely tufted, the tufts thickly scattered over the spots, rupturing the epidermis, simple, straight or almost so, arising from a loose to compact stroma, olive-brown to Dresden brown, $10-30 \times 4-5 \mu$, continuous, conidial scars fairly distinct. Conidia obclavate, curved, Dresden brown, $20-75 \times 5-7.5 \times 2-3 \mu$, 2-6-7 septate.

On leaves of **Fraxinus* sp. (?)

Specimens examined: Ellis and Everhart, N. Amer. Fungi, Sec. Ser., No. 1525 (type) (Decorah, Iowa).

Cercospora bolleana (Thümen) Spegazzini, Mich., 1: 475, 1879. On *Ficus carica* L., Briosi and Cavara, I Funghi Parass., No. 85 (Pavia, Italy).

Cercospora cerasella Saccardo, Mich., 1: 266, 1879. On *Prunus virginiana* L., Bartholomew, Fungi Columb., No. 1608 (Rooks Co., Kan.)

Cercospora desmodii Ellis and Kellerman, Bull. Torr. Bot. Club, 11: 121, 1884. On *Desmodium* sp., Ellis and Everhart, N. Amer. Fungi, Sec. Ser., No. 1501 (Manhattan, Kan.).

Cercospora rosaecola Passerini, in Thümen's Myc. Univ., No. 333, 1876. On *Rosa blanda* Ait., Bartholomew, Fungi Columb., No. 3412 (London, Ontario, Canada).

Cercospora simulata Ellis and Everhart, 1: 64, 1885. On *Cassia marilandica* L., Ellis and Everhart, N. Amer. Fungi, Sec. Ser., No. 1751 (Granville, Mass.).

Cercospora umbrata Ellis and Holway, Jour. Myc., 2: 2, 1886. On *Bidens* sp., Ellis and Everhart, N. Amer. Fungi, Sec. Ser., No. 1521 (type) (Decorah, Ia.).

SECTION VI

Mycelium internal, conidiophores simple, stroma composed of loosely to fairly compactly interwoven hyphae, or rarely none produced, conidia cylindrical or somewhat fusiform.

Cercospora cana Saccardo, Myc. Ven., No. 593, 1876; Nuovo Giorn. Bot. Ital., 8: 188, 1876.—Rábenhorst, Fungi Europaei, No. 2153, 1876; Hedw., 15: 119, 1876.—Saccardo, Fungi Ital., Pl. 68, 1877; Mich., 1: 88, 1877.—Frank, Krankh. d. Pfl., pp. 593–601, 1880. Figs. 107, 108, 110.—Ellis and Everhart, Jour. Myc., 1: 54, 1885.

Syn. *Cercosporella cana* (Saccardo) Saccardo, Mich., 2: 364, 1881; Syll. Fung., 4: 218, 1886.—Costantin, Les Mucédinées Simples, p. 74, 1888. Fig. 36²⁻³.—Davis, Trans. Wis. Acad., 11: 166, 1898.—Kellerman, Jour. Myc., 9: 172, 1903; Ohio Fungi, No. 142, 1906.—Lindau in Rabenhorst's Kryptogamen-Flora, 8: 429, 1907. Fig. 2.—Davis, Trans. Wis. Acad., 16: 742, 1910; 17: 889, 1914; 21: 257, 1924.

Fusidium canum Passerini, in Thümen, Myc. Univ., No. 378, 1876.

Type locality: Selva, Italy, P. A. Saccardo, Aug. 1875, Myc. Ven., No. 593, Rabenhorst, Fungi Europaei, No. 2153.

Spots amphigenous, mostly definite, rarely indefinite, subcircular to somewhat angular, more or less vein-limited, at times confluent, 1–6 mm., light green at first, becoming light yellowish-green, light brown to dark brown, darker above than below, frequently appearing grayish to grayish-white, especially on the lower surface, due to the abundance of conidiophores and conidia, margin at times greenish; border indefinite. Mycelium internal, subhyaline, rarely light Dresden brown, 1.5–4.5 μ , stromatic mycelium subhyaline to light to dark Dresden brown, 2.5–9 μ . Conidiophores amphigenous, or in some cases hypophyllous, moderately tufted, emerging through the stomata, simple, or very rarely branched, straight below, substraight to prominently geniculate in region of conidial production, arising from a loose to compact stroma, subhyaline to light greenish-yellow, 20–106 \times 3–6 μ , continuous or 1–3 septate, conidial scars distinct, prominently denticulate, closely aggregated towards the tips, or more rarely somewhat scattered. Conidia oblong-cylindrical to narrowly obclavate, straight or somewhat curved, subhyaline to light greenish-yellow, 25–100–140 \times 3.5–6.5 \times 2.5–4 μ , continuous or 1–5–9 somewhat distantly septate.

On leaves of **Erigeron* sp., **E. canadensis* L., **E. annuus* (L.) Pers.,

E. philadelphicus L., *E. ramosus* (Walt.) BSP., **Solidago* sp., and *S. canadensis* L.

The position of the conidiophores on the upper and lower surfaces of the leaves is correlated with the particular host species. On *E. canadensis* they are abundant on both surfaces, on *E. annuus* they are mostly hypophyllous, and on the species of *Erigeron* in Ellis' N. Amer. Fungi, No. 1248, they are present only on the lower surface. On *Solidago* they are abundant on both surfaces of the leaves.

The fungus on *Solidago*, Herb. Univ. of Ill. ex Coll. Mo. State Univ., No. 20219, differed from the forms on *Erigeron* in that the conidial scars were scattered in the former and aggregated towards the tips in the latter. This difference is quite possibly due to different growth conditions and since the various specimens agreed in all other respects it is perhaps not of any significance.

It is impossible to say with absolute certainty whether Passerini or Saccardo first named this species. The first publication in a journal was by Saccardo, Nuovo Giorn. Bot. Ital., April 30, 1876. However, this publication was antedated by Passerini as Saccardo calls attention to *Fusidium canum* Pass. in a note to his species. The date of publication, therefore, depends on whether Saccardo's Myc. Ven. Cent. VI was issued before Thümen's Myc. Univ. Cent. VI. Both were issued early in 1876, apparently before April 30. Since Saccardo retains his name calling attention to Passerini's it is perhaps right to assume that Myc. Ven. Cent VI was issued the earlier of the two exsiccati. Lindau (l. c.) has apparently adopted this view, giving Saccardo credit for the species.

Specimens examined: As *Cercospora cana* Sacc., Rabenhorst, Fungi Europaei, No. 2153 (type) (Selva, Treviso, Italy).—Rabenhorst-Winter, Fungi Europaei, Ser. II, No. 3290 (Amanda, Ohio).—Ellis, N. Amer. Fungi, No. 1248 (Amanda, Ohio).—Herb. Univ. of Ill. ex Coll. Mo. State Univ., No. 20219 (Columbia, Mo.). As *Cercospora cana* (Sacc.) Sacc., Sydow, Myc. Ger., No. 1171 (Brandenburg).—Ellis and Everhart, Fungi Columb., No. 595 (Port Byron, Ill.).—Seymour and Earle, Ec. Fungi, Nos. 310 (Middlebush, N. J.) and 312 (New Brunswick, N. J.).—Kellerman, Ohio Fungi, No. 142 (Buckeye Lake, Ohio).—Bartholomew, Fungi Columb., Nos. 2918 (London, Canada) and 4009 (Ithaca, N. Y.). As *Fusidium canum* Pass., Thümen, Myc. Univ., No. 378 (type) (Parma, Italy).

Cercospora carotae (Passerini) Solheim n. sp.

Syn. *Cercospora apii* Fresenius var. *carotae* Passerini, Mem. R. Acad. Linnei, Roma, IV ser., 6: 469, 1890.—Saccardo, Syll. Fung., 10: 624, 1892.—v. Höhnelt, Ann. Myc., 1: 530, 1903.—Lindau in Rabenhorst's Kryptogamen-Flora, 9: 125, 1910.

Type locality: Parma, Italy.

Spots amphigenous and cauliculus, subcircular on the leaves, oblong-elliptical on the stems, more or less vein-limited and confluent, 0.3–3 mm. on the leaves, 1–4×1 mm. on the stems, light brown to dark brown, usually lighter in color towards the centers of the spots than at edges; border definite, more or less raised, dark purplish-brown, 45–150 μ , the whole at times surrounded by a very narrow yellow translucent area. Mycelium internal, hyaline, 1.5–6 μ , the larger hyphae obtaining beneath the conidiophores. Conidiophores amphigenous, solitary or loosely tufted, emerging through the stomata or rupturing the epidermis, simple, straight to subflexuous, with or without a bulbous or inflated base, non-stromatic, light yellowish-brown, 15–45×3–5 μ , continuous; conidial scars minute, rather indistinct, mostly aggregated towards the tips. Conidia at first cylindrical, then narrowly-obclavate, bacilliform, hyaline to subhyaline, 30–115×2–3×1.5 μ , continuous or obscurely 1–8 septate.

On leaves and stems of **Daucus carota* L.

The original description calls for conidiophores hyaline, septulate; conidia 30–65×3.5–4 μ . The conidiophores of the specimens examined were not hyaline but the color was very dilute. It is quite probable that they are hyaline when young. Just what is meant by septulate is difficult to say. Since no septa were observed it may be taken to mean that there was some doubt as to whether or not septa were actually present.

This fungus is distinctly different from *C. apii* Fresen. The conidia are much shorter and narrower. The septa are indistinct and the distance between them is about twice that in the conidia of *C. apii* Fresen. The conidiophores are equally distinct.

Specimens examined: Sydow, Myc. Ger., No. 1043 (Brandenburg).—Ellis and Everhart, N. Amer. Fungi, Sec. Ser., Nos. 2482a (Emma, Mo.) and 2482b (New Brunswick, N. J.).—Seymour and Earle, Ec. Fungi, No. 442 (New Brunswick, N. J.).

Cercospora pastinacae (Saccardo) Peck, Bull. N. Y. State Mus., 157: 45, 107, 1912.—Ellis and Everhart, Jour. Myc., 1: 37, 1885, sub *Cercospora apii*.

Syn. *Cercospora apii* Fresenius var. *pastinacae* Saccardo, Syll. Fung., 4: 442, 1886.

Type locality: ?

Spots amphigenous, inconspicuous, sub-angular to irregular, vein-limited, at times confluent, 0.5–2 mm., yellowish-green, rusty-brown to tan above, olivaceous to light yellowish-brown below; border indefinite. Mycelium internal, irregular, hyaline to subhyaline, 1.5–4.5 μ , stromatic mycelium dilute yellowish-brown, 4.5–7 μ . Conidiophores amphigenous, loosely to somewhat densely tufted, the tufts being uniformly scattered over the spots, emerging through the stomata, simple, flexuous, inflated

as they emerge from the host, arising from a stroma of loosely to somewhat compactly interwoven hyphae, light olive-brown to yellowish-brown $15-76 \times 4-7\mu$, continuous, or 1 septate near bases; conidial scars distinct, scattered, warty. Conidia acicular, fusiform, straight or curved, light greenish-yellow, $30-95 \times 4-5.5 \times 2-3\mu$, continuous to distantly 1-3 septate. [Fig. 14.]

On leaves of **Pastinaca sativa* L.

Peck lists the conidia as being $25-85 \times 6-8\mu$ which is slightly different from the above measurements.

Ellis and Everhart referred this fungus to *C. apii* Fresen. but stated that it was perhaps specifically distinct. Later Saccardo gave it the name of *C. apii* Fresen. var. *pastinacae* Sacc. Peck examining the fungus in 1912 concluded that it was a distinct species. His conclusion is undoubtedly correct. The spots produced, the conidiophores and conidia, of this fungus differ markedly from those of *C. apii* Fresen.

Specimens examined: Ellis and Everhart, N. Amer. Fungi, Sec. Ser., No. 1739b (Columbia, Mo.).—Seymour and Earle, Ec. Fungi, No. 443 (New Brunswick, N. J.).—Thümen, Herb. Myc. Oec., No. 321 (Bayreuth, Bavaria). On the last specimen two kinds of spots were present, one of which appeared to be due to *C. pastinacae* (Sacc.) Peck. However, no fruiting bodies could be found.

Cercospora pastinacina Solheim n. name and n. comb.

Syn. *Cercosporaella pastinacae* Karsten, Hedw., 23: 63, 1884.—Saccardo, Syll. Fung., 4: 219, 1886. Kirchner, Krank. u. Beschäd. unsers Land. Kulturpflanzen, p. 396, 1906.—Lindau, in Rabenhorst's Kryptogamen-Flora, 8: 424, 1907.—Cotton, Kew Bull. Misc. Inf., 1918, p. 19, fig. 2.

Type locality: Mustiala, Finland.

Spots amphigenous, subcircular, more or less confluent, 0.5-3 mm., at first brown, then becoming white centered; border definite, slightly raised, brown, $50-200\mu$. Mycelium internal, hyaline to subhyaline, $1.5-4.5\mu$, individual cells frequently irregular in outline. Conidiophores amphigenous, indistinct, densely tufted, scattered in vein-limited sectors of the spots, rupturing the epidermis, simple, straight to subfluous, tapering, arising from a short compact stroma, subhyaline to very dilute yellowish, $14-30 \times 2-3\mu$, continuous; conidial scars fairly distinct, aggregated at tips. Conidia narrowly-obclavate, bacilliform, subhyaline to dilute yellowish, $20-110 \times 1-2.5 \times 0.8-1.5\mu$, obscurely 1-6 septate.

On leaves of **Pastinaca sativa* L.

No cross walls were observed in the conidiophores. From the nature of the material it was, however, impossible to determine whether or not they never are present.

This fungus has been confused with *C. pastinacae* (Sacc.) Peck. The

reason for this is apparently due to a misconception of what the latter actually is since the two are quite distinct.

Since the genus *Cercospora* already contains a valid species bearing the name *C. pastinacae* (Sacc.) Peck, it is necessary to secure a new name for the above described fungus. *C. pastinacina* Solheim is the name given it.

Specimens examined: As *C. apii* Fresen., Ellis and Everhart, Fungi Columb., No. 885b (London, Canada). As *C. apii* Fresen. var. *pastinacae sativae*, Thümen, Myc. Univ., No. 1169 (Bayreuth, Bavaria).

Cercospora campi-silii Spegazzini, Mich., 2: 171, 1880.—Saccardo, Syll. Fung., 4: 440, 1886.—Lindau in Rabenhorst's Kryptogamen-Flora, 9: 115, 1910. Ann. Myc., 25: 286, 1927.

Type locality: Consiglio, Italy.

Spots amphigenous, angular to subcircular, more or less vein-limited, at times confluent, 1–5 mm; smaller spots grayish-green above, larger spots tri-colored, with a grayish-green center surrounded by a tan-colored zone which in turn is surrounded by a darker brown border above, similar below but somewhat brownish throughout; border indefinite or definite, slightly raised, brown, 50–350 μ . Mycelium internal, fairly regular, subhyaline, 1.6–3.2–4.9 μ , in diameter. Conidiophores amphigenous but mostly hypophyllous, solitary or loosely to somewhat densely tufted, emerging through the stomata or rupturing the epidermis, simple, or rarely with opposite branches, erect, subflexuous to flexuous, non-stromatic, dilute olivaceous, 30–100–140 \times 3.2–6.5 μ , continuous or somewhat obscurely 1, rarely 2, septate; conidial scars distinct, mostly shouldered, at times denticulate, scattered. Conidia cylindrical to fusiform, subhyaline to dilute olivaceous, 15–50 \times 2–3.5 \times 1.6–3.5 μ , up to 6.5 μ at the widest point, 1–6 somewhat irregularly septate.

On leaves of **Impatiens nolitangere* L.

One conidium was observed germinating and producing a conidiophore.

The conidiophores of specimen No. 2034, Sydow, Myc. Ger., were not infrequently branched. The branching, however, was not uniformly distributed but confined to certain sectors on the spots. The conidiophores of the other specimens listed were not branched.

Specimens examined: Sydow, Myc. Ger., No. 2034 (Schröpfung, Brandenburg). Krypt. Exs., No. 2040 (Tullnerbach, Austria).

Cercospora dubia (Riess) Winter, Hedw., 22: 10, 1883. On *Chenopodium album* L., Bartholomew, Fungi Columb., No. 4211 (Ithaca, N. Y.).

Cercospora granuliformis Ellis and Holway, Jour. Myc., 1: 6, 1885. On *Viola cucullata* Ait., Ellis and Everhart, Fungi Columb., No. 445 (Nuttallburg, W. Va.).

Cercospora maianthemi Fuckel, Symb. Myc., p. 353, 1869. On *Maianthemum convallaria* Web., Rabenhorst-Winter, Fungi Europari, Ser. II, No. 3590a (Borussia near Halle, Germany).

Cercospora osmorrhizae Ellis and Everhart, Proc. Nat. Acad. Sci. Phil., p. 89, 1891. On *Osmorrhiza longistylis* (Torr.) DC., Ellis and Everhart, Fungi Columb., No. 458 (Racine, Wis.).

Cercospora toxicodendri Ellis, Am. Nat., 16: 811, 1882. On *Rhus toxicodendron* L., Ellis and Everhart, N. Amer. Fungi, Sec. Ser., No. 1524 (Newfield, N. J.).

SECTION VII

Mycelium internal, conidiophores with opposite branching, stroma composed of loosely to fairly compactly interwoven hyphae, or rarely none produced, conidia abruptly obclavate.

Cercospora cercidicola Ellis, Am. Nat., 16: 810, 1882; Jour. Myc., 1: 36, 1885.—Saccardo, Syll. Fung., 4: 463, 1886.—Atkinson, Jour. Elishu Mitch. Sci. Soc., 8: 42, 1891.—Halsted, N. J. Agr. Exp. Sta. Rept., 1896, p. 397, figs. 45–47.—Schwarze, N. J. Bull., 313: 132, 1917, figs. 789–791.—Anderson U. S. Dept. Agr. Bull., 1366: 33, 1926.

Syn. *Cercospora cercidicola* Ellis var. *coremioides* Tehon, Myc., 16: 140, 1924. Pl. 13, fig. 11.

Type locality: Lexington, Ky., W. A. Kellerman, 1882, Ellis N. Amer. Fungi, No. 1246.

Spots amphigenous, circular to angular, vein-limited, 1–4 mm., blackish-brown to rusty-brown becoming grayish above but remaining rusty-brown beneath; border definite, raised, black to black-brown, 75–150 μ , the whole surrounded by a reddish or brown to rusty-brown zone. Mycelium internal, hyaline to subhyaline, 1–4.5 μ , stromatic mycelium olive-brown, 3–7 μ . Conidiophores amphigenous but mostly hypophyllous, coremioid, loosely to rather densely tufted, emerging through the stomata or rupturing the epidermis, straight for about one-half to three-fourths their length, very flexuous throughout remainder of their length, arising from a small stroma of compactly interwoven hyphae, olive-brown, 50–280 \times 3–5 μ , 1–8 septate, more or less branched, branches mostly opposite and subtending a terminal conidial scar, rarely monopodially branched below the region of conidial production and then subtending a septum, conidial scars distinct, prominently denticulate, collected towards tips. Conidia obclavate, straight or curved, olivaceous, 20–55 \times 4–6.5 \times 2–3 μ , distinctly 1–3 septate. [Fig. 5.]

On leaves of **Cercis canadensis* L., *C. japonica* Sieb., and *C. occidentalis* Torr.

The coremioid character on which *C. cercidicola* Ell. var. *coremioides* Tehon is based is characteristic of the species.

This fungus appears to be closely related to *C. petersii* (B. and C.) Atk., having the same habit of growth and the same type of conidia and conidiophores.

Specimens examined: Ellis, N. Amer. Fungi, No. 1246 (type) (Lexington Ky.).—Bartholomew, Fungi Columb., No. 3306. (Cabin John Bridge, Md.).

SECTION VIII

Mycelium internal, conidiophores with alternate branching, stroma tuberculate, conidia acicular-obclavate.

Cercospora heucherae Ellis and Martin, Am. Nat., 18: 189, 1884.—Ellis and Everhart, Jour. Myc., 1: 34, 1885.—Saccardo, Syll. Fung., 4: 453, 1886.—Davis, Trans. Wis. Acad., 9: 166, 1893.

Type locality: Chester Co., Pa., Ellis, N. Amer. Fungi, No. 1258.

Spots amphigenous, circular, convex above, concave below, scattered over the leaf, 1.5–5 mm.; uniformly brown to dark-brown or with a tan-colored center, at times with a reddish tint above, similar below but lighter and somewhat olive-tinted; border definite surrounding the tan center when present as well as the major spot, dark-brown, very narrow, 15–25 μ , the whole surrounded by a yellowish, at times red-tinted, halo, 30–90 μ to 1 mm. Mycelium internal, somewhat regular to very irregular, much branched, hyaline to olive-brown, more or less guttulate, 1.5–4.6 μ in diameter. Conidiophores amphigenous, densely tufted, the tufts somewhat scattered over the spots, rupturing the epidermis or emerging through the stomata, intricately branched towards the bases, branching penicillioid, the whole forming a compact tubercle-like structure capped by the ultimate branches (25–50 \times 3.5–4.5 μ) which superficially appear to be the complete conidiophores, somewhat flexuous, geniculate, yellowish-brown to olive-brown, 35–100 \times 3.5–5 μ , closely septate in tuberculate region, continuous to 1–2 septate in superficial region. Conidia narrowly obclavate, rarely acicular, hyaline to light greenish-yellow, 10–115 \times 2.5–3.5 \times 1.5–2.5 μ , 2–14 septate.

On leaves of **Heuchera americana* L. and *Heuchera* sp.

Germinated conidia were observed on the spots. Germ tubes emerged at the base and tip and also at the sides. The tubes traversed the epidermis until they came to stomata through which they made entrance into the host.

The branching of the conidiophores of this species is very distinct. It much resembles that of *Penicillium* from which it differs in that it is at the basal end of the conidiophore. Superficial examination does not reveal the branching but gives the impression that the fungus is an ordinary unbranched *Cercospora* with a stroma. The tubercle-like formation produced by the compact conidiophores indicates that the true *Cercospora*

tubercle is perhaps formed from the basal portion of the conidiophores instead of the mycelium.

Specimens examined: Ellis, N. Amer. Fungi, No. 1258 (type) (Chester Co., Pa.).—Herb. Univ. of Ill. *ex* Herb. F. L. Stevens, Ohio Fungi, Nos. 40 (Marblehead, L. Erie) and 181 (Sciota River, O.).

Cercospora rhoïna Cooke and Ellis, Grev., 6: 89, 1878.—Ellis and Everhart, Jour. Myc., 1: 33, 1885.—Saccardo, Syll. Fung., 4: 467, 1886.—Atkinson, Jour. Eli. Mitch. Sci. Soc., 8: 47, 1891.—Carver, Proc. Ia. Acad., 8: 165, 1900.—Schwarze, N. J. Bull., 313: 140, 1917. figs. 832–836.

Syn. *Cercospora copallina* Cooke, Grev., 12: 31, 1883.—Saccardo, Syll. Fung., 4: 468, 1886.

Type locality: New Jersey. Kew No. 2656.

Spots amphigenous, suborbicular to irregular, more or less vein-limited, tan-colored, dark-brown, blackish-brown, purplish-brown or reddish-brown above, light-brown to dark-brown, or reddish-brown below, in age sometimes becoming greyish, border indefinite or definite and dark brown to purplish, somewhat raised, the surrounding leaf tissue usually with a reddish discoloration. Mycelium internal, 2.5–4 μ in diameter, much branched, subhyaline to light yellowish brown, the darker color obtaining especially beneath the tufts of tuberculate conidiophores. Conidiophores amphigenous, densely tufted, emerging through the stomata or rupturing the epidermis, tuberculate, somewhat branched at or near the bases, rarely above, straight to subflexuous, geniculate, olive-brown, 20–100 \times 3–4 μ , septate towards the bases. Conidia oblong-cylindrical to narrowly fusoid or obclavate-acicular, more or less curved, subhyaline to light olive-yellow, 30–160 \times 3–4 \times 1.6–3.0 μ , obscurely 3–14 septate.

On leaves of **Rhus glabra* L., **R. copallina* L., **R. typhina* L., *R. pumila* Michx., *R. toxicodendron* L., *R. vernix* L., *R. canadensis* Marsh. and *R. sp.*

The branching and septation of the conidiophores are a little difficult to observe due to the dense tufts. Sections as well as masseration after boiling, however, bring these points out very clearly. In the specimens examined the longest conidiophores noted were 100 μ . Atkinson records them up to 150 μ .

The specimen recorded as *C. rhoïna* Cooke and Ellis, on *Rhus aromatica*, Sydow, Fungi Exot. Exs., No. 447, is immature. Although the spots resemble those produced by this fungus, it can not definitely be said that the causal organism is *C. rhoïna* Cooke and Ellis. Roumeguère, Fungi Sel. Exs., No. 4387, recorded as *C. rhoïna* Cooke and Ellis, is mislabeled. Beyond this the material did not permit of further determination.

Only one specimen of the fungus on *Rhus typhina*, Herb. Univ. of Ill., No. 32982, *ex* Herb. U. S. Dept. of Agric., Div. of V. P. P., No. 1815, has been seen. This specimen lacked conidia. The spots, mycelium, and con-

diophores were all typical of *C. rhoina* and the determination is in all probability correct.

In comparing the type collection of *C. copallina* Cooke in Ravenel, Fungi Amer. Exs., No. 586, as well as other collections with various collections of *C. rhoina* Cooke and Ellis, the difference between the two as inferred by Cooke was not observed. Both have the same types of spots, mycelium, olive-brown tuberculate conidiophores, and obscurely septate, obclavate-acicular conidia. Ellis and Everhart, Jour. Myc., 1: 34, 1885, could find no difference between the two. *C. copallina* Cooke must, therefore, be considered a synonym of *C. rhoina* Cooke and Ellis.

Specimens examined: As *C. rhoina* Cooke and Ellis, Ellis, N. Amer. Fungi, No. 47 (Newfield, N. J.); No. 1252 (Manhattan, Kan.).—Ellis and Everhart, Fungi Columb., No. 794 (Newfield, N. J.).—Bartholomew, Fungi Columb., No. 2613 (Lincoln, Neb.); No. 2809 (Rogers, Ark.); No. 4613 (Tallahassee, Fla.).—Roumeguère, Fungi Gallici Exs. No. 3876 (Manhattan, Kan.).—Seymour and Earle, Ec. Fungi, No. 119 (Granville, Mass.).—Herb. Univ. of Ill. ex Herb. Univ. of Wis., specimen collected by J. J. Davis at Lynxville, Wis., Aug. 31, 1915; Herb. Univ. of Ill., No. 32982 ex Herb. U. S. Dept. of Agric., Div. of V. P. P., No. 1815. (Washington, D. C.). As *C. copallina* Cooke, Ravenel, Fungi Amer. Exs., No 586 (Aiken, S. C.).—Ellis and Everhart, N. Amer. Fungi, Sec. Ser., No. 1505 (Green Cove Springs, Fla.).—Rabenhorst and Winter, Fungi Europaei, Ser. II, No. 3682 (Green Cove Springs, Fla.).—Herb. Univ. of Ill. ex Herb. A. B. Seymour, specimen collected by G. Martin at Green Cove Springs, Fla., Dec. 1884.

Cercospora ribicola Ellis and Everhart, Proc. Acad. Sci. Phil., p. 379, 1894. On *Ribes sanguineum* Pursh., Ellis and Everhart, N. Amer. Fungi, Sec. Ser., No. 3391 (Seattle, Wash.).

SECTION IX

Mycelium internal, conidiophores with alternate branching, stroma tuberculate, conidia cylindrical.

Cercospora smilacis Thümen, Instituto de Coimbra, 27: 24, 1879; Hedw., 19: 135, 1880; Myc. Univ., Nos. 1670 and 1768, 1880.—Saccardo, Syll. Fung., 4: 476, 1886.—Overholts, Ann. Mo. Bot. Gard., 14: 428, 1927. Pl. 40.

Type locality: Coimbra, Portugal, Thümen, Myc. Univ., No. 1768; prototype, Myc. Univ., No. 1670.

Spots amphigenous, circular to angular, more or less vein-limited, at times confluent, 0.5–5 mm., dark-brown, somewhat darker above than below; border definite, raised, dark-brown to blackish-brown on inner margin, light to dark brown on outer margin, 75–200 μ . Mycelium internal, very

irregular, hyaline to olive-brown, 2–7.5 μ , forming here and there compact stromatic mats, stromatic mycelium dark olive-brown, 4.5–10 μ . Conidiophores amphigenous but mostly hypophyllous, densely tufted, rupturing the epidermis, with a bulbous base, flexuous, arising from a large, compact, tuberculate stroma, Brussels brown 25–140 \times 4.5–6 μ , 1–5 septate, somewhat branched, branches well developed each producing several conidia, conidial scars more or less obscure, somewhat warty, scattered. Conidia oblong-cylindrical to narrowly obclavate, olivaceous, 20–125 \times 3–4.5 \times 2–4.5 μ , continuous or 1–10 septate. [Fig. 9.]

On leaves of **Similax mauritanica* L.

Overholts lists conidiophores up to 225 μ and conidia to 135 μ .

The conidia germinate in two ways, either they produce an infecting mycelium or they produce conidiophores directly.

This species differs from *C. petersii* (B. and C.) Atk. in having branched, erect, but not coremioid conidiophores and much narrower conidia.

C. similacis Thüm., Ellis, N. Amer. Fungi, No. 1251, does not belong under this species. It does not appear to agree with any of the described species of *Cercospora* on *Smilax*. However, until further studies can be made of these species it is advisable to leave it as now designated.

Specimens examined: Thümen, Myc. Univ., Nos. 1670 (prototype) and

Tyype) (Coimbra, Portugal).—Rabenhorst-Winter, Fungi Europaei, Ser. II, No. 2975 (Coimbra, Portugal).—Roumeguère, Fungi Sel. Exs., No. 5189 (Coimbra, Portugal).

SECTION X

Mycelium internal, conidiophores with alternate branching, stroma composed of loosely to fairly compactly interwoven hyphae, or rarely none produced, conidia cylindrical.

Cercospora consociata Winter, Hedw., 22: 70, 1883.—Ellis and Everhart, Jour. Myc., 1: 53, 1885.—Saccardo, Syll. Fung., 4: 470, 1886.

Type locality: Illinois, A. B. Seymour.

Spots amphigenous, angular, vein-limited, 4–10 mm., more or less sunken below and correspondingly raised above, dark grayish-brown to smoky-brown; border indefinite, or in part definite, not raised or slightly raised, blackish-brown, 0.0–500 μ . Mycelium internal, more or less verrucose, hyaline to very dilute olivaceous, 1.5–3.5 μ , stromatic mycelium olive-brown, 2.5–6 μ . Conidiophores amphigenous, loosely to moderately tufted, emerging through the stomata, underlate with a more or less bulbous base, arising from a loose to somewhat compact stroma, light olive-brown, 20–55 \times 3–4.5 μ , 1–4 septate, conidial scars indistinct, scattered, branched monopodially at or near the base, less frequently above, two or more branches may develop on a single conidiophore, branches well de-

veloped, producing several conidia. Conidia oblong-cylindrical to bacilli-form, very slightly thickened below, greenish-yellow, $35-130 \times 2-3.5 \times 1.5-2\mu$, 2-8 septate.

On leaves of **Ruellia ciliosa* Pursh.

The above description differs from the original in recording the conidiophores as being amphigenous. The original description states that they are hypophyllous.

Specimens examined: Ellis and Everhart, N. Amer. Fungi, Sec. Ser., No. 2477 (Emma, Mo.).

Cercospora lateritia Ellis and Halsted, Jour. Myc., 4: 7, 1888. On *Sambucus racemosa* L., Ellis and Everhart, N. Amer. Fungi, Sec. Ser., No. 1994. (type) (Ames, Ia.).

Cercospora lupini Cooke, Hedw., 17: 39, 1878. On *Lupinus diffusus* Nutt., Ravenel, Fungi Amer. Exs., No. 67 (Aiken, S. Car.).

SECTION XI

Mycelium internal, conidiophores with alternate and opposite branching, stroma composed of loosely to fairly compactly interwoven hyphae, or rarely non-produced, conidia cylindrical.

Cercospora illinoensis Bartholomew, Fungi Columb., No. 2611, 1908.—Saccardo, Syll. Fung., 22: 1428, 1913.

Type locality: Farmington, Ill., E. Bartholomew, No. 3696, Sept. 18, 1907

Spots indefinite, conidiophores effused in velvety, olive-brown to Brussels brown patches below, the leaf tissue above the patches becoming yellowish to brown and dotted with scattered tufts of conidiophores, the latter being especially grouped along the veins. Mycelium internal, hyaline, subhyaline to Dresden brown, $1-4.5-6\mu$, stromatic mycelium up to 7.5μ . Conidiophores amphigenous, loosely to moderately tufted below, rather densely tufted above, emerging through the stomata below, rupturing the epidermis above, straight to subflexuous, more or less geniculate, arising from a loose to somewhat compact stroma, Brussels brown, $30-265 \times 3-4.5\mu$, at times up to 6μ towards tips, 2-25 septate, branched, the branches irregularly alternate, or opposite and subtended by a terminal conidial scar, well developed, conidial scars distinct, laterally displaced and warty or shouldered, aggregated towards the tips. Conidia oblong-cylindrical, tapering slightly, straight or somewhat curved, light yellowish-olive, Dresden brown to Prout's brown, $25-115 \times 3.5-6 \times 2.5-5\mu$. 1-10-13 septate. [Fig. 8.]

On leaves of **Asclepias syriaca* L.

Specimens examined: As *Cercospora illinoensis* Barth., Bartholomew, Fungi Columb., No. 2611 (type) (Farmington, Ill.).—Specimen collected

at Urbana, Ill., Sept. 9, 1927 (culture study). As *Cercospora clavata* (Ger.) Peck, Bartholomew, Fungi Columb., No. 4006 (Ithaca, N. Y.).—Farlow, Reliquiae Farlowianae, No. 161 (Newton, Mass.).

Cercospora fusco-virens Saccardo, Mich., 2: 149, 1880. On *Passiflora lutea* L., Rabenhorst-Winter, Fungi Europaei, Ser. II, No. 3586 (Perryville Mo.).

SECTION XII

Mycelium internal and external, conidiophores simple, stroma tuberculate, conidia acicular-obclavate.

Cercospora helianthemis Briosi and Carvara, I Funghi Parass., No. 334, 1900. figs. 1–3.—Traverso, Malpighia, 14: 478, 1900.—Lindau in Rabenhorst's Kryptogamen-Flora, 9: 120, 1910.—Saccardo, Syll. Fung., 22: 1414, 1913.

Type locality: Pavia, Italy, Briosi and Cavara, I Funghi Parass., No. 334.

Spots amphigenous, circular, more or less confluent, greatly hypertrophied, 0.5–2 mm., brown above, becoming grayish centered, below olivaceous; border definite but distinguishable only in section, raised. Mycelium external and internal; external mycelium regular to irregular, the cells frequently of irregular outline, hyaline to light olivaceous, 1.5–7.5 μ ; internal mycelium very irregular, hyaline to light olivaceous to yellowish-brown, 1.5–5 μ , stromatic mycelium 4.5–6 μ . Conidiophores amphigenous, moderately to densely tufted, emerging through the stomata, more rarely rupturing the epidermis, or sparsely scattered on the external mycelium, straight to subflexuous, or somewhat flexuous towards the tips, arising from a compact tuberculate stroma, Brussels brown, 25–215 \times 4–6.5 μ , continuous or 1–5 septate, somewhat branched, the branches of monopodial origin, more or less scalariform, conidial scars distinct, scattered or somewhat aggregated at various points on the conidiophores, more or less shouldered. Conidia acicular, hyaline, 25–160 \times 2.5–4 \times 1.5–2 μ , closely 1–18 septate.

On leaves of *Helianthemum* sp. and **H. polifolium* DC. var. *roseum* Wk.

The external mycelium of this fungus is rather difficult to see. Only with the use of the oil immersion lens is it clearly brought out. The branched conidiophores may also quite readily be overlooked.

Specimens examined: Briosi and Cavara, I Funghi Parass., No. 334 (type) (Pavia, Italy).

Cercospora ilicis Ellis, Bull. Torr. Bot. Club, 8: 65, 1881. On *Ilex glabra* (L.) Gray, Ellis, N. Amer. Fungi, No. 548 (type). (No locality given.)

SECTION XIII

Mycelium internal and external, conidiophores simple, stroma tuberculate, conidia abruptly obclavate.

Cercospora condensata Ellis and Kellerman, Jour. Myc., 1: 2, 1885; Hedw., 24: 127, 1885.—Ellis and Everhart, Jour. Myc., 2: 2, 1886.—Saccardo, Syll. Fung., 4: 438, 1886.—Davis, Trans. Wis. Acad., 18: 267, 1916.

Type locality: Manhattan, Kans., W. A. Kellerman, July 1884. Prototype, Manhattan, Kans., W. A. Kellerman, Sept. 1884, Ellis and Everhart, N. Amer. Fungi, Sec. Ser., No. 1518.

Spots amphigenous, irregular, vein-limited, 0.5–1.5 mm., dark brown to brown, becoming whitish centered; border definite, raised, dark brown, 100–200 μ . Mycelium external and internal; external mycelium arising from the internal and emerging through the stomata, olivaceous, 3–6 μ , somewhat irregularly constricted at septa; internal mycelium hyaline to yellowish, very fine, 1–3 μ ; stromatic mycelium olive-brown to blackish-brown, 3–7.5 μ . Conidiophores amphigenous, densely tufted below, much more so above, emerging through the stomata, rupturing the epidermis, or scattered on the external mycelium, simple, straight to subflexuous, arising from a large tuberculate stroma, olive-brown, 30–70 \times 4–6 μ , continuous, or 1–2 septate, conidial scars minute, distinct, subdentate, aggregated towards the tips. Conidia obclavate to narrowly obclavate, straight or somewhat curved, olive-brown, 40–160 \times 3–6 \times 2–3 μ , 6–15 septate, at times slightly constricted at septa.

On leaves of **Gleditschia triacanthos* L.

In the specimen distributed in Seymour and Earle, Ec. Fungi, No. 121, the conidiophores had apparently had two distinct periods of growth. The portion developed in the second period was practically hyaline as compared with the fairly deep olive-brown portion previously produced.

Specimens examined: Ellis and Everhart, N. Amer. Fungi, Sec. Ser., No. 1518 (prototype) (Manhattan Kans.).—Seymour and Earle, Ec. Fungi, No 121 (Havana, Ill.).

Cercospora petersii (Berkeley and Curtis) Atkinson, Jour. Elishu Mitch. Sci. Soc., 8: 57, 1891; Ala. Bull., 80: 149, 1897. Sub *Cercospora smilacis* Thümen, Peck, 33 Rept. N. Y. State Mus., p. 29, 1880. Pl. 2, figs. 1–3.—Ellis and Everhart, Jour. Myc., 1: 33, 1885.—Davis, Trans. Wis. Acad., 21: 274, 1924. Sub *Cercospora smilacina* Sacc., Overholts, Ann. Mo. Bot. Gard., 14: 429, 1927. Pl. 41.

Syn. *Helminthosporium petersii* Berkeley and Curtis, Grev., 3: 102, 1874.—Saccardo, Syll. Fung., 4: 421, 1886.

Type locality: Carolina, Berkley, N. Amer. Fungi, No. 626.

Spots amphigenous, circular to somewhat angular, more or less vein-limited, at times confluent, 0.5–4 mm., reddish-brown, purplish-brown to blackish-brown; border definite, raised, dark reddish-brown to blackish-brown on inner margin, light brown to fairly dark brown on outer margin, 150–325 μ , leaf tissue surrounding spot generally discolored. Mycelium internal and external; external mycelium verrucose, olivaceous to olive-brown, 1.5–4.5 μ ; internal mycelium very irregular, cells irregularly inflated, hyaline, olivaceous, to olive-brown, 1.5–9 μ ; stromatic mycelium Dresden brown to olive-brown, 3–12 μ . Conidiophores amphigenous but mostly hypophyllous, coremioid, moderately to somewhat densely tufted, rupturing the epidermis, or very sparsely scattered on the external mycelium, simple, with a bulbous base, straight for about two-thirds their length, distal one-third divergent and profusely subflexuous to flexuous, arising from a somewhat loose to compact tuberculate stroma, argus brown, Dresden brown, Prout's brown to blackish-brown, 50–230 \times 3–6 μ , 1–8 septate, conidial scars small, fairly distinct, somewhat warty, aggregated towards tips. Conidia obclavate, with a more or less bulbous tip, olive-brown, 25–90 \times 4–6 \times 1.5–3.5 μ , continuous or 1–7–11 septate, closely septate towards bases, distantly septate towards tips. [Fig. 11.]

On leaves of **Smilax glauca* Walt., **S. rotundifolia* L., **S. sps.*, *S. hispida* Muhl., *S. tamnoides* Gray, *S. laurifolia* L., and *Benzoin aestivale* (L.) Nees.

Atkinson lists conidiophores to 300 μ and conidia to 100 μ .

The conidia were germinating abundantly on all the specimens examined. Germination was mostly from the basal cell although quite common from the other cells as well. Conidia were frequently observed anastomosing. At times the conidia germinated producing short hyphae which in turn produced conidia.

This fungus has commonly been confused with *C. smilacis* Thüm. and *C. smilacina* Sacc. This confusion is undoubtedly due to Peck's misinterpretation of *C. smilacis* Thüm. and his description and drawings based on this wrong conception. The two fungi are quite distinct. (See *C. smilacis* Thüm., l. c.), Saccardo has placed Peck's fungus under the species *C. smilacina* Sacc. It is also distinct from the latter species (l. c.).

Specimens examined: As *Helminthosporium petersii* B. and C., Ravenel, Fungi Amer. Exs., Nos. 166 and 616 (Aiken, S. Car.). As *Cercospora smilacis* Thüm., Ellis and Everhart, Fungi Columb., No. 390 (Newfield, N. J.).—Herb. Univ. of Ill., No. 33002, ex Herb. U. S. Dept. Agric., No. 616 (Kanawaha Falls, W. Va.). As *C. smilacina* Sacc., Seymour and Earle, Ec. Fungi, No. 199 (Big Stone Gap, Va.).—Herb. Univ. of Ill., A. B. Seymour, Plainville, Ct. Aug. 27, 1883. As *C. mississippiensis* Tracy and Earle, Bartholomew, Fungi Columb., No. 2808 (Batesville, Ark.).

Cercospora gymnocladii Ellis and Kellerman, Bull. Torr. Bot. Club, 11: 121, 1884. On *Gymnocladus dioica* (L.) Koch, Bartholomew, Fungi Columb., No. 2212 (Grand Island, Neb.). [Fig. 4.]

SECTION XIV

Mycelium internal and external, conidiophores simple, stroma tuberculate, conidia cylindrical.

Cercospora acrocomiae Stevenson, Rep. Ins. Exp. Sta., Porto Rico, 7: 89, 1917.

Type locality: Rio Piedras, Porto Rico, July 1914, No. 2090; Feb. 1912, (Johnston) No. 4206; July 1917, No. 6604 (type).

Spots amphigenous, few, areas between spots dying out so as to make large, continuous, dead areas, circular to elliptical, 5–20 mm. long by 3–6 mm. broad, rarely wider, at first reddish-brown, then tricolored, a central circular to elliptical gray area, $2-6 \times 0.5-3$ mm., enclosed by a blackish-brown band 2–3 mm. wide, with an outer more or less irregular reddish-brown to brown area, often not completely encircling the central portions; border indefinite. Mycelium external and internal; external mycelium arising from the internal and emerging through the stomata, irregular, olive-brown, $1.5-6\mu$; internal mycelium irregular, somewhat verrucose, olive-brown, darker than the external and mostly coarser, $2-9\mu$; stromatic mycelium dark Dresden brown to olive-brown, $2-9\mu$. Conidiophores amphigenous but mostly hypophyllous, confined to the central gray areas of the spots, densely tufted, rupturing the epidermis, simple, straight to subflexuous, irregularly inflated or constricted, arising from a large tuberculate stroma, Argus brown, enlarged towards the tips, i.e., tapering from tips towards bases, $30-160 \times 3-5\mu$, up to 7.5μ at tips, 2–9 septate, conidial scars indistinct. Conidia oblong cylindrical, straight, curved or doubly curved, Brussels brown to Prout's brown, $40-130 \times 6-12 \times 6-12\mu$, 4–12 closely septate.

On leaves of **Acrocomia media* Cook.

Specimens examined: Herb. Univ. of Ill., No. 4206a, collected by John R. Johnston, Rio Piedras. Porto Rico, Feb, 14, 1912.

Cercospora silphii Ellis and Everhart, Jour. Myc., 4: 3, 1888. On *Silphium integrifolium* Michx., Ellis and Everhart, Fungi Columb., No 456 (Rockfort, Kan.).

SECTION XV

Mycelium internal and external, conidiophores simple, stroma composed of loosely to fairly compactly interwoven hyphae, or rarely none produced, conidia acicular-obclavate.

Cercospora sorghi Ellis and Everhart, Jour. Myc., 3: 15, 1887.—Saccardo, Syll. Fung., 10: 656, 1892.—Carver, Proc. Ia. Acad., 8: 165, 1900.

Type locality: Plaquemines Co., La., Aug. 1886. Langlois, No. 543.

Leaves at first stained dark purple, in strips of several inches in extent, the affected part becoming dead and dry, the centers of the strips becoming grayish brown, the edges remaining purple. Mycelium internal and external; external mycelium very regular, subhyaline, $1.0\text{--}2.0\mu$; internal mycelium very irregular, the adjacent cells frequently varying considerably in size and shape, subhyaline to light brown, $1\text{--}6.5\mu$. Conidiophores amphigenous, loosely tufted, emerging through the stomata or very rarely arising from the external mycelium, simple, straight or becoming subflexuous towards the tips, arising from a compact stroma, Dresden brown, $35\text{--}145 \times 3.2\text{--}5.0\mu$, 1–4 septate, conidial scars distinct, more or less shouldered, mostly grouped on the upper half of the conidiophore. Conidia acicular or somewhat cylindrical when young, subhyaline, $45\text{--}240 \times 2\text{--}3.2 \times 1\text{--}1.5\mu$, somewhat obscurely 5–20 septate.

On leaves of **Sorghum halapense* (L.) Pers., *S. vulgare* Pers., and *Zea mays* L.

Specimens examined: Ellis and Everhart, N. Amer. Fungi, Sec. Ser., No. 1768 (Point a la Hache, La.).

Cercospora rubi Saccardo, Nuovo Giorn. Bot. Ital., 8: 188, 1876. On *Rubus trivialis* Michx., Ellis and Everhart, N. Amer. Fungi, Sec. Ser., No. 1740 (St. Gabial, La.).

SECTION XVI

Mycelium internal and external, conidiophores simple, stroma composed of loosely to fairly compactly interwoven hyphae, or rarely none produced, conidia abruptly obclavate.

Cercospora ampelopsidis Peck, Rept. N. Y. State Mus., 30: 55, 1878.—Ellis and Everhart, Jour. Myc., 1: 55, 1885.—Saccardo, Syll. Fung., 4: 459, 1886.—Davis, Trans. Wis. Acad., 21: 289, 1924.

Syn. *Cercospora pustula* Cooke, Grev., 12: 30, 1883. Saccardo, Syll. Fung., 4: 458, 1886.

Type locality: Bethlehem, N. Y., C. H. Peck, July.

Spots amphigenous, circular to angular, more or less vein-limited, 1–8 mm., at first blackish to reddish-black, becoming reddish-brown to brown above, below brown, raw umber, Saccardo's umber to olive-brown; border indefinite or definite, at times definite above and indefinite below, raised, black to brownish-black above, dark brown below, 0.2–1 mm., the whole frequently surrounded by a reddish discolored area. Mycelium internal and external; external mycelium regular to irregular, subhyaline to dilute raw umber, arising from the internal and emerging with the tufts of

conidiophores, 0.8–3–4.5 μ ; internal mycelium hyaline, olivaceous to dilute raw umber, occasionally producing groups of beaded cells, 1.5–4.5–6 μ ; stromatic mycelium olive-brown, Dresden brown to raw umber, 3.5–7.5 μ . Conidiophores amphigenous, loosely to moderately tufted, emerging through the stomata or rupturing the epidermis, simple, or rarely irregularly branched, straight to flexuous, at times somewhat undulate, with a more or less bulbous base, arising from a loose to compact stroma, Brussels brown, Prout's brown, raw umber to olive-brown, 35–215 \times 3–6 μ , 2–10 septate, conidial scars laterally displaced and somewhat warty to denticulate, or at times shouldered. Conidia at first cylindrical, then abruptly obclavate, straight or somewhat curved, olivaceous, light Dresden brown to raw umber, 20–115 \times 3–5–6.5 \times 1.5–3 μ , 1–7–15 septate, distinctly septate towards bases, somewhat obscurely septate towards tips.

On leaves of **Parthenocissus* sp., *P. quinquefolia* Planch., *P. quinquefolia* Planch. var. *hirsuta* Planch.

The specimen distributed in Roumeguère, Fungi Sel. Exs., No. 5589, had no fruiting fungus on it. The spots present did not in any respect resemble those described above.

Specimens examined: As *Cercospora ampelopsidis* Peck, Rabenhorst-Winter, Fungi Europaei, Ser. II, No. 3291 (Bethlehem, Pa.).—Seymour and Earle, Ec. Fungi, No. 7 (Urbana, Ill.).—Ellis and Everhart, N. Amer. Fungi, Sec. Ser., No. 1748 (West Chester, Pa.).—Bartholomew, Fungi Columb., No. 3506 (London, Canada).—Specimen collected at White Heath, Ill., July 23, 1927 (culture study). As *Cercospora pustula* Cooke, Ravenel, Fungi Amer. Exs., No. 779 (type) (Darien, Ga.).—Ellis and Everhart, N. Amer. Fungi, Sec. Ser., No. 2474 (St. Martinsville, La.).

Cercospora olivacea (Berkeley and Ravenel) Ellis, Jour. Myc., 1: 52, 1885. On *Gleditschia triacanthos* L., Rabenhorst-Winter, Fungi Europaei, Ser. II, No. 2974 (Fulton Co., Ill.).

Cercospora thalictri Thümen, Cont. Fl. Mycol. Lusit., p. 5, 1878. On *Thalictrum flavum* L., Thümen, Myc. univ., No. 1470 (type) (Coimbra, Portugal).

SECTION XVII

Mycelium internal and external, conidiophores with alternate branching, stroma tuberculate, conidia abruptly obclavate.

Cercospora glomerata Harkness, Bull. Calif. Acad. Sci., 3: 164, 1885.—Kellerman, Jour. Myc., 1: 106, 1885.—Saccardo, Syll. Fung., 4: 472, 1886.

Type locality: Tamalpais, Calif., H. W. Harkness, March, 1884,

No. 3651. Prototype, H. W. Harkness, Tamalpais, Calif., March, 1884, Ellis and Everhart, N. Amer. Fungi, Sec. Ser., No. 1641.

Spots amphigenous, angular, spreading from the margin of the leaf inward or originating on the main portion of blade, 1–17 mm., brown, becoming grayish-brown, the lower surface dotted with black punctiform tufts of conidiophores; border definite, slightly raised, tan colored, or brown of a darker shade than that of the main spot. Mycelium external and internal; external mycelium hyaline to Prout's brown, the colored portion more or less verrucose, $1.5\text{--}6\mu$; internal mycelium subhyaline, yellowish-green to Prout's brown, $1.5\text{--}4.5\mu$; stromatic mycelium Prout's brown, $2\text{--}6\mu$. Conidiophores hypophyllous, very rarely epiphyllous, more or less confined to vein-limited sectors of the spots, densely tufted, emerging through the stomata and later rupturing the surrounding epidermis, subflexuous to flexuous, arising from a large structure the lower part of which is composed of a tuberculate stroma above which is a long broad body made up of somewhat loosely interwoven, much branched, more or less parallel hyphae, Prout's brown to Brussels brown, $25\text{--}90 \times 3\text{--}5.5\mu$, 2–8 closely septate towards bases, monopodially branched, the branches irregularly placed but mostly near the bases, at times short and again long and well developed, producing several conidia, conidial scars more or less indistinct, laterally displaced or rarely shouldered, slightly warty. Conidia obclavate, abruptly attenuated but only slightly so, apical cell rounded, Dresden brown, $25\text{--}77 \times 4.5\text{--}7.5 \times 3\text{--}4.5\mu$, 1–5–7 septate, more or less constricted at septa.

On leaves of **Garrya elliptica* Dougl.

The original description gives the diameter of the conidia as $10\text{--}12\mu$. In the specimens examined, both collected at the type locality, no conidia were observed as thick as this.

Specimens examined: Ellis and Everhart, N. Amer. Fungi, Sec. Ser., No. 1641 (prototype) (Tamalpais, Calif.).—Rabenhorst-Winter, Fungi Europaei, Ser. II, No. 3792 (Tamalpais, Calif.).

SECTION XVIII

Mycelium internal and external, conidiophores with alternate branching, stroma composed of loosely to fairly compactly interwoven hyphae, or rarely none produced, conidia acicular-obclavate.

Cercospora sordida Saccardo, Mich., 2: 149, 1880; Fungi Ital., Pl. 683, 1881; Syll. Fung., 4: 470, 1886.—Ellis and Everhart, Jour. Myc., 1: 53, 1885.—Atkinson, Jour. Elishu Mitch. Sci. Soc., 8: 63, 1891.

Type locality: Georgia, Ravenel.

Spots more or less indefinite, the tufts of conidiophores forming olive-brown, vein-limited patches, or covering the whole of the lower surface of

the leaf, the upper leaf surface above the patches of conidiophores becoming first dark green, then yellowish. Mycelium internal and external; the external mycelium regular, subhyaline to olivaceous, arising from the conidiophores, or from the internal mycelium and emerging with the tufts of conidiophores, 1.5–3 rarely 4.5 μ ; internal mycelium hyaline, subhyaline, olivaceous or yellowish-olive, 1.5–4.5–6 μ , at times forming dark olive-brown tuberculate structures near the upper leaf surface. Conidiophores hypophyllous, emerging through the stomata, or effused on the external mycelium, loosely tufted, straight, subflexuous or flexuous, non-stromatic or arising from a very small stroma, Dresden brown to yellowish-olive, 15–110 \times 3–5 μ , at times somewhat enlarged towards the tips, up to 4.5–7.5 μ , continuous or 1–5 irregularly septate, at times somewhat constricted, irregularly branched, the branches usually well developed, conidial scars indistinct, rarely shouldered. Conidia oblong-cylindrical to narrowly obclavate, greenish-yellow, olivaceous to Dresden brown, 20–190 \times 3–4.5 \times 2–3.5 μ , 2–15 fairly distinctly septate, at times slightly constricted at septa.

On leaves of *Tecoma radicans* (L.) Juss.

Numerous conidia were observed germinating. The germ tube was sent out from any point on the conidium but if a conidium was placed over or just to the side of a stoma it always arose from the point closest to the stoma. Occasionally conidia were observed to germinate and produce conidiophores directly.

Cercospora duplicata Ellis and Everhart, Jour. Myc., 5: 70, 1889, has not been seen. It is quite probable, however, that it is the epiphyllous expression of the above described fungus.

Specimens examined: Ellis, N. Amer. Fungi, No. 1247 (Newfield, N. J.).—Bartholomew, Fungi Columb., Nos. 2315 (Louisville, Kan.), 2812 (Batesville, Ark.), 4212 (Shreveport, La.), and 4514 (Spiro, Okla.).—Rabenhorst-Winter, Fungi Europaei, Ser. II, No. 3794 (Perryville, Mo.).—Seymour and Earle, Ec. Fungi, No. 146 (Starkville, Miss.).

Cercospora acerina Hartig, Lehrb. d. Baumkrankh., p. 113, 1882. On *Acer pseudoplatanus* Falk., Briosi and Cavara, I Funghi Parass., No. 296 (Vallombrosa, Italy).

Cercospora lini Ellis and Everhart, Jour. Myc., 3: 16, 1887. On *Linum virginianum* L., Ellis and Everhart, N. Amer. Fungi, Sec. Ser., No. 1762 (Faulkland, Del.).

SECTION XIX

Mycelium internal and external, conidiophores with alternate branching, stroma composed of loosely to fairly compactly interwoven hyphae, or rarely none produced, conidia abruptly obclavate.

Cercospora ferruginea Fuckel, in Fresenius, Beitr., 3: 93, 1863; Hedw., 2: 134, 1863; 3: 20, 1864; Symb. Myc., 1: 354, 1869; 2: 20, 1873.—Frank, Krankh. d. Pfl., p. 601, 1880.—Saccardo, Fungi Ital., Pl. 655, 1881; Syll. Fung., 4: 444, 1886.—Grove, Jour. Bot., 24: 204, 1886.—Keissler, Ann. Myc., 5: 233, 1907.—Lindau in Rabenhorst's Kryptogamen-Flora, 9: 139, 1910.

Syn. *Helminthosporium absinthium* Peck, 30 Rept. N. Y. State Mus., p. 54, 1878. pl. 2, figs. 28–30.

Cercospora absinthii (Peck) Saccardo, Syll. Fung., 4: 444, 1886.—

Davis, Trans. Wis. Acad., 18: 269, 1916.

Type locality: Rhineland, Fuckel.

Spots indefinite, the conidiophores forming effused brown patches on the lower surface of the leaf, the upper leaf surface above the patches becoming somewhat yellowish. Mycelium internal and external; external mycelium arising from the internal and emerging through the stomata, fine; internal mycelium fine. Conidiophores hypophyllous, rarely epiphyllous, loosely to moderately tufted, emerging through the stomata, or effused on the external mycelium, flexuous, brown, $60\text{--}400 \times 4\text{--}6\mu$, at times somewhat swollen towards the tips, 1 to several septate, monopodially branched, branches well developed, conidial scars fairly distinct, laterally displaced, aggregated towards the tips. Conidia abruptly obclavate, very variable in size, especially in thickness, yellowish, $21\text{--}102 \times 4\text{--}10\mu$, 1–3–6 septate. [Fig. 6.]

On leaves of **Artemisia vulgaris* L., **A. absinthium* L., *A. japonica* Thumb., *A. ludoviciana* Nutt., *A. suksdorfii* Piper, and *A. vulgaris* L. var. "indica."

The conidia of this species are quite variable in size, especially in thickness. Measurements of the conidia of various specimens are as follows: $24\text{--}102 \times 5\text{--}7\mu$, $26\text{--}100 \times 5\text{--}7\mu$, $25\text{--}88 \times 4\text{--}6\mu$, $21\text{--}67 \times 6\text{--}8\mu$, $28\text{--}75 \times 5\text{--}9\mu$, $28\text{--}78 \times 7\text{--}10\mu$. Keissler reports a specimen with conidia $35\text{--}40 \times 10\text{--}15\mu$.

The fungus described as *Helminthosporium absinthium* by Peck and later referred to *Cercospora* by Saccardo, on *Artemisia absinthium*, is undoubtedly the same as *Cercospora ferruginea* Fckl. Peck's species appears to have been based on young material. A comparison of several specimens of the two revealed no differences. *C. absinthii* (Peck) Sacc., therefore, becomes a synonym of *C. ferruginea* Fckl.

The fungi referred to this species on *Teucrium*, *Erigeron*, and *Ambrosia* do not belong here. They are quite distinct and do not appear to even be closely related.

Specimens examined: As *Cercospora ferruginea* Fckl., Rabenhorst, Fungi Europaei, Nos. 766 (Hostrichia), 1286 (Brünn, Moravia), and 2152

(Selva, Treviso, Italy).—Sydow, Myc. Ger., Nos. 1195 (Lohringen, Germany) and 1775 (Brandenburg, Germany).—Thümen, Myc. Univ., No. 286 (Selva, Treviso, Italy). *Cercospora absinthii* (Pk.) Sacc., Ellis and Everhart, N. Amer. Fungi, Sec. Ser., No. 1770 (Newfield, N. J.); Fungi Columb., No. 1363 (London, Canada).

Cercospora concors (Caspary) Saccardo, Syll. Fung., 4: 449, 1886. On *Solanum tuberosum* L., Rabenhorst-Winter, Fungi Europaei, Ser. II, No. 3790 (Königstein, Germany).

Cercospora menispermii Ellis and Holway, Jour. Myc., 4: 6, 1888. On *Menispermum canadense* L., Ellis and Everhart, Fungi Columb., No. 596 (Nuttallburg, W. Va.).

Cercospora passaloroides Winter, Hedw., 22: 71, 1883. On *Amorpha canescens* Pursh, Ellis and Everhart, N. Amer. Fungi, Sec. Ser., No. 1999 (Manhattan, Kan.).

SECTION XX

Mycelium internal and external, conidiophores with alternate branching, stroma composed of loosely to fairly compactly interwoven hyphae, or rarely none produced, conidia cylindrical.

Cercospora portoricensis Earle, Muhlenbergia, 1: 16, 1901.—Saccardo, Syll. Fung., 18: 609, 1906.—Stevens, Trans. Ill. State Acad., 10: 212, 1917.

Syn. *Cercospora piperis* Ellis and Everhart, 9th Ann. Rept. Mo. Bot. Gard., p. 119, 1898. Not Patouillard.

Cercospora pipericola Saccardo and Sydow, Syll. Fung., 16: 1073, 1902.

Type locality: *Cercospora portoricensis* Earle, Mayaguez, Porto Rico, Herb. New York Bot. Gard., No. 4359, A. A. Heller. *Cercospora piperis* Ellis and Everhart, Port Morant, Jamaica, Herb. Mo. Bot. Gard., No. 22343, A. S. Hitchcock.

Spots amphigenous, irregular, oblong, or subcircular, vein-limited, more or less confluent, 1–7 mm., greenish, olive-brown, rusty-brown, dark-brown or grayish-black above, similar below but appearing olivaceous due to abundance of conidiophores; border indefinite. Mycelium internal and external; external mycelium regular, fine, 1.5–3 μ , subhyaline to light olivaceous, arising from the internal mycelium and emerging through the stomata, or arising from the conidiophores; internal mycelium irregular, 1.5–6 μ , hyaline, subhyaline to light olivaceous. Conidiophores hypophyl-

lous, at times amphigenous, loosely to somewhat densely tufted, emerging through the stomata or scattered on the external mycelium, straight to subflexuous, spreading, non-stromatic or loosely stromatic, Dresden brown to olivaceous to fairly dark olive-brown, $15-125 \times 3-5\mu$, continuous or irregularly 1-6 septate, not infrequently with adjacent cells of unequal diameter, branched, the branches arising from any point on the conidiophore, mostly at right angles and, when more than one, all on the same side; conidial scars indistinct. Conidia oblong-cylindrical to narrowly-obclavate, light brownish-yellow to olivaceous, $25-120 \times 2.5-4-5 \times 2-3.5\mu$, at first continuous, later somewhat irregularly 1-10 septate, guttulate. [Fig. 13.]

On leaves of *Piper* sps., **P. aduncum* Auct., **P. hispidum* Sw., **P. peltatum* L., and **P. umbellatum* L.

Epiphyllous conidiophores were rare and observed only on *P. hispidum* and *P. peltatum*.

The type materials of *C. portoricensis* Earle and *C. piperis* Ell. and Ev. have been examined and compared. No essential difference exists between the two. The slight differences that do exist, such as shades of color, size of conidia and conidiophores, appear to be due to differences in age in the specimens. *C. piperis* Ell. and Ev. is based on very young material, while *C. portoricensis* Earle is based on old material. Both specimens show the same type of external and internal mycelium; they have conidia and conidiophores structurally alike and branched in the same manner. *C. piperis* Ell. and Ev. must, therefore, drop into synonymy. *C. portoricensis* Earle becomes the name of the fungus, since *C. piperis* Pat. antedates *C. piperis* Ell. and Ev., thus invalidating the latter name.

Specimens examined: As *C. piperis* Ell. and Ev., Herb. Mo. Bot. Gard., No. 22343 (type) (Port Morant, Jamaica) (Courtesy of Mo. Bot. Gard.). As *C. portoricensis* Earle, Herb. N. Y. Bot. Gard. No. 4359 (type) (Mayaguez, Porto Rico) (Courtesy of N. Y. Bot. Gard.).—Herb. Univ. of Ill., J. A. Stevenson, Nos. 3315 (Bayamon, Porto Rico) and 2867 (Rio Piedras, Porto Rico); Herb. Univ. of Ill., Porto Rican Fungi, Nos. 7035 (Mayaguez), 9131 (Juana Diaz), 146 (Caoma) and 7133 (Porto Rico).

Cercospora agerati Stevens, Bull. Bernice P. Bishop Mus., 19: 154, 1925. On *Ageratum conyzoides* L., Herb. Univ. of Ill., Hawaiian Fungi, No. 944 (Kealakakua).

Cercospora amorphophalli Hennings, Hedw., 41: 147, 1902. On *Amorphophallus campanulatus* Blume., Herb. Univ. of Ill., specimen collected by M. B. Raimundo, Nov. 1, 1913, Los Bunos, Philippine Islands.

SECTION XXI

Mycelium internal and external, conidiophores with alternate and opposite branching, stroma composed of loosely to fairly compactly interwoven hyphae, or rarely none produced, conidia cylindrical.

Cercospora lobeliaecola Solheim, n. name. On *Lobelia cardinalis* L., Ellis and Everhart, N. Amer. Fungi, Sec. Ser., No. 1516 (Manhattan, Kan.).

This fungus has been known as *C. effusa* (B. & C.) Ell. [= *Cladosporium effusum* B. & C.]. The specific name given by Berkeley and Curtis rightly belongs to the fungus on *Polygonum punctatum* described by these authors. This fungus has been known as *Cercospora hydropiperis* (Thüm.) Speg. It is now referred to *Didymaria* as *D. effusa* (B. & C.) Solheim, n. comb. (l.c.). A new specific name is, therefore, necessary for the fungus on *Lobelia* and *C. lobeliaecola* is chosen.

DIDYMARIA (CORDA) *emend.* SOLHEIM

Didymaria Corda, Icon. Fung., 5: 9, 1842; Anleit., p. 32, 1842; Icon. Fung., 6: 8, 1854.—Saccardo, Syll. Fung., 4: 184, 1886.—Masee, British Fungus-Flora, 3: 340, 1893.—Schroeter in Cohn, Krypt. Flora v. Schlesien, 3: 2: 484, 1897.—Lindau, in Engler and Prantl, Nat. Pflanzenfam., 1: 1: 445, 1900 and in Rabenhorst's Kryptogamen-Flora, 8: 377, 1907.

ORIGINAL DESCRIPTION

"Flocci entophyllini, repentis, continui, sporis acrogenis, heterogenis, didymis, dien inspersis."

EMENDED DESCRIPTION

Conidiophores tufted, emerging through the stomata or rupturing the epidermis, simple or branched, more or less geniculate, straight or flexuous, continuous or septate, arising from a loose to compact or tuberculate stroma, hyaline to dark brown. Conidia acrogenous, at times appearing lateral due to further development of the conidiophores, clavate, at first continuous, later becoming one or more septate, hyaline to dark brown.

The type species is *Didymaria didyma* (Unger) Schroeter.

Didymaria didyma (Unger) Schroeter, in Cohn, Krypt. Flora v. Schlesien 3: 2: 484, (1897) 1908.—Lindau, in Rabenhorst's Kryptogamen-Flora, 8: 378, 1907. 2 figs.

Syn. *Ramularia didyma* Unger, Exanth., p. 169, 1833. Pl. II, fig. 10.—

Ellis and Everhart, Jour. Myc., 1: 81, 1885.

Didymaria ungeri Corda, Anleit., p. lviii. Pl. B. 9, fig. 1, 1842.—

Saccardo, Fungi Ital., Pl. 969, 1881; Syll. Fung., 4: 184, 1886.—

Masee, British Fungus-Flora, 3: 340, 1893. fig. 17, p. 274.

Type locality: ?

Spots subcircular to angular, vein-limited, 2–10 mm., at first dark blackish-brown, becoming lighter with one or more concentrically zoned areas variously placed which are greenish, greenish-brown or light brown, the zone bands are raised and somewhat darker than the intervening spaces; border mostly indefinite, rarely definite and then slightly raised and blackish-brown. (On *Anemone virginiana* the spots are brown above and light yellowish below, there is no concentric zonation, and the border is indefinite.) Mycelium internal, rarely external; external mycelium emerging through the stomata, very sparse, hyaline to subhyaline, $1.5\text{--}2\mu$; internal mycelium subhyaline to dilute greenish-yellow, $1.2\text{--}2.5\mu$. Conidiophores hypophyllous, rupturing the epidermis (emerging through the stomata on *Anemone virginiana*), moderately to densely tufted, with a slightly bulbous base, simple, or rarely branched, straight to somewhat flexuous, geniculate, non-stromatic to very loosely stromatic, hyaline to dilute yellowish, $30\text{--}125 \times 3\text{--}4.5\mu$, 1–2 septate, conidial scars distinct, scattered. Conidia clavate, hyaline to dilute yellowish, $15\text{--}40 \times 3\text{--}7.5 \times 4.5\text{--}11\mu$, at first continuous, becoming 1-septate. [Fig. 16.]

On leaves of *Ranunculus* sp., **R. repens* L., **R. septentrionalis* Poir., *R. "acer,"* *R. lanuginosus* L., *R. lingua* L., *R. nemorosus* DC., *R. pennsylvanicus* L., *R. polyanthemus* L., and **Anemone virginiana* L.

The form on *Anemone virginiana* gave spore measurements of $15\text{--}35 \times 3\text{--}6 \times 4.5\text{--}9\mu$, whereas the forms on *Ranunculus* sps. measured $20\text{--}40 \times 4.5\text{--}7.5 \times 7\text{--}11\mu$. The conidial scars on the former were slightly denticulate. This was not noted in the *Ranunculus* specimens. These slight differences may or may not be significant. The host reaction differences noted in the description do not appear to have much value as differentiation characters. The stomata of the host species examined are different enough to readily account for the emergence of the conidiophores through them in one case and the rupturing of the epidermis in the other.

Specimens examined: As *Didymaria didyma* (Ung.) Schroet., Sydow, Myc. Ger., No. 1769 (Brandenburg, Germany).—Kryptogamae Exs., No. 1486 (Wurzbachtal, Austria).—Migula, Crypt. Ger., Aust., et Helv. Exs., No. 280 (Eisenach, Thuringia, Germany). As *D. ungeri* Corda, Roumeguère, Fungi Gall. Exs., No. 3487 (Fontainebleau, France).—Ellis and Everhart, Fungi Columb., No. 158 (London, Canada). As *Ramularia didyma* Ung., Thümen, Myc. Univ., No. 2076 (Carniolia; Laibach).—Ellis and Everhart, N. Amer. Fungi, Sec. Ser., No. 1529 (Decorah, Iowa).

Didymaria effusa (Berkeley and Curtis) Solheim, n. comb.

Syn. *Cladosporium effusum* Berkeley and Curtis, Grev. 3: 106, 1875.

Cercospora polygonorum Cooke, Hedw., 17: 39, March, 1878.

—Ellis and Everhart, Jour. Myc., 1: 52, 1885.

Cercospora hydropiperis (Thümen) Spegazzini, Anal. de la Soc. Cien. Argentina, Buenos Aires, 9: 191, 1880.—Saccardo, Syll. Fung., 4: 455, 1886.—Carver, Proc. Ia. Acad., 8: 164, 1900.—Kellerman, Jour. Myc. 8: 58, 1902; Ohio Fungi, No. 65.—Spegazzini, Bol. Acad. Nac. Cordoba, 23: 529, 1919.

Helminthosporium hydropiperis Thümen, Myc. Univ., No. 1087, 1878.

Type locality: Society Hill, S. Carolina, Ravenel, Herb. Royal Botanic Garden, Kew, No. 3775.

Spots more or less indefinite, the upper surface of the leaf above the spots occupied by the patches of conidiophores at first becoming pale yellowish, later dark-brown to reddish-brown, below yellowish to brown, the latter obscured by the abundance of conidiophores which give the lower surface of the leaf an olive-brown to Prout's brown, velvety appearance, the patches at first subcircular, then coalescing and eventually becoming effused over the whole lower surface of the leaf; border indefinite. Mycelium internal, irregular, very abundant, subhyaline to olive-brown, $1.5-9\mu$, stromatic mycelium subhyaline to olive-brown, $3-6.5\mu$. Conidiophores amphigenous but mostly hypophyllous, loosely so moderately tufted, densely aggregated, straight, somewhat undulate, simple or rarely monopodially branched, arising from a loose to compact or even tuberculate stroma, Prout's brown to Dresden brown, $25-140 \times 3.5-5\mu$, somewhat enlarged towards tips, up to 7.5μ , continuous or 1-10 septate, conidial scars more or less indistinct, scattered, laterally displaced, occasionally shouldered. Conidia clavate, straight or curved, yellowish, dilute yellowish-brown to dilute Dresden brown, $20-85 \times 3-6 \times 4.5-9\mu$, at first continuous, becoming 1-6-10 somewhat irregularly septate. [Fig. 15.]

On leaves of **Polygonum acre* HBK., **P. hydropiper* L., **P. hydropiperoides* Michx., *P. pennsylvanicum* L., and *P. sp.*

Germination of several conidia was observed. This occurred most frequently from the basal and apical cells, although from the others as well. From the apical cell the germ tube emerged directly from the tip and grew directly away from it. In the basal cell the germ tube arose either at the top of the cell and then grew at right angles to it, or it arose just next to the scar of attachment and then curved away from the conidium and proceeded parallel to it but in the opposite direction.

On several of the specimens pycnidial or perithecial-like bodies were present in the older spots. That these belong to the fungus in question is evident. They arose from the same mycelium as the conidiophores, and not infrequently tufts of conidiophores originated in them, either from the globose portion or from the wall surrounding the ostiole. These bodies are globose, ostiolate, dark olive-brown, and measure $25-70\mu$ in diameter.

The type specimen, *Cladosporium effusum* B. and C., Kew, No. 3775, has been examined. In this specimen most of the mature conidia have fallen off. A few, however, were present, showing this specimen to be the same in all respects as the type specimens and others recorded under the synonymy listed above.

Specimens examined: As *Cladosporium effusum* B. and C., Herb. Royal Botanic Garden, Kew., No. 3775 (type), courtesy of the Royal Botanic Garden, Kew) (Society Hill, S. Car.). As *Helminthosporium hydropiperis* Thüm., Thümen, Myc. Univ., No. 1087 (type) (Aiken, S. Car.). As *Cercospora hydropiperis* (Thüm.) Speg., Roumeguère, Fungi Gall. Exs., No. 3994 (Jersey City, N. J.).—Ellis and Everhart, Fungi Columb., No. 391 (Port Byron, Ill.).—Bartholomew, Fungi Columb., Nos. 2311 (London, Canada); 2707 (Loup City, Neb.); and 3208 (Luray, Va.).—Kellerman, Ohio Fungi, No. 65 (Columbus, Ohio). As *C. polygonorum* Cooke, Ravenel, Fungi Amer. Exs., No. 66 (type) (Aiken, S. Car.).—Rabenhorst-Winter, Fungi Europaei, Ser. II, Nos. 3289a (Perryville, Mo.) and 3289b (Cobden, Ill.).—Seymour and Earle, Ec. Fungi, Nos. 370a (Millstone, N. J.) and 370b (Meriden, Ct.).—Ellis, N. Amer. Fungi, No. 549 (Delaware Co., Pa.).

HOST INDEX

- Acalypha gracilens* Gray
 Cercospora acalyphae Peck
Acalypha ostryaefolia Riddel
 Cercospora acalyphae Peck
Acalypha virginica L.
 Cercospora acalyphae Peck
Acer pseudoplatanus Falk.
 Cercospora acerina Hart.
Acnida cannabina L.
 Cercospora acnidae Ell. & Ev.
Acrocomia media Cook
 Cercospora acrocomiae Stevenson
Ageratum conyzoides L.
 Cercospora agerati Stev.
Alisma plantago-aquatica L.
 Cercospora alismatis Ell. & Holw.
Alternanthera achyrantha R. Br.
 Cercospora alternantherae Ell. & Lang.
Alternanthera portoricensis Kuntze
 Cercospora alternantherae Ell. & Lang.
Amorpha canescens Pursh
 Cercospora passaloroides Wint.
Amorphophallus companulatus Blume
 Cercospora amorphophalli Henn.
Anemone virginiana L.
 Didymaria didyma (Ung.) Schroet.
Apios tuberosa Moench.
 Cercospora tuberosa Ell. & Kell.
Apium graveolens L.
 Cercospora apii Fresen.
Apium graveolens rapaceum DC.
 Cercospora apii Fresen.
Arachis hypogaea L.
 Cercospora personata (B. & C.) Ell.
Arctium lappa L.
 Cercospora arctii Stev.
Artemisia absinthium L.
 Cercospora ferruginea Fckl.
Artemisia japonica Thunb.
 Cercospora ferruginea Fckl.
Artemisia ludoviciana Nutt.
 Cercospora ferruginia Fckl.
Artemisia suksdorfii Piper
 Cercospora ferruginea Fckl.
Artemisia vulgaris L.
 Cercospora ferruginea Fckl.
Artemisia vulgaris L. var. *indica*
 Cercospora ferruginea Fckl.
Asclepias incarnata L.
 Cercospora clavata (Ger.) Peck
Asclepias syriaca L.
 Cercospora illinoensis Barth.
Benzoin aestivale (L.) Nees
 Cercospora petersii (B. & C.) Atk.
Beta vulgaris L.
 Cercospora beticola Sacc.
Bidens sp.
 Cercospora umbrata Ell. & Holw.
Bupleurum tenuissimum L.
 Cercospora bupleuri Pass.
Cassia marilandica L.
 Cercospora simulata Ell. & Ev.
Cassia occidentalis L.
 Cercospora occidentalis Cooke
Cercis canadensis L.
 Cercospora cercidicola Ell.
Cercis japonica Sieb.
 Cercospora cercidicola Ell.
Cercis occidentalis Torr.
 Cercospora cercidicola Ell.
Chenopodium album L.
 Cercospora dubia (Riess) Wint.
Clematis virginiana L.
 Cercospora squalidula Peck
Crotalaria sagittalis L.
 Cercospora demetroniana Wint.
Daucus carota L.
 Cercospora carotae (Pass.) Solheim
Desmanthus illinoensis (Michx.) MacM.
 Cercospora desmanthi Ell. & Kell.
Desmodium sp.
 Cercospora desmodii Ell. & Kell.
Echinocystis lobata (Michx.) T. & G.
 Cercospora echinocystis Ell. & Mart.
Erigeron sp.
 Cercospora cana Sacc.
Erigeron annuus (L.) Pers.
 Cercospora cana Sacc.

- Erigeron canadensis* L.
Cercospora cana Sacc.
Erigeron philadelphicus L.
Cercospora cana Sacc.
Erigeron ramosus (Walt.) BSP.
Cercospora cana Sacc.
Euonymus japonicus L.
Cercospora destructiva Rav.
Eupatorium album L.
Cercospora ageratoides Ell. & Ev.
Eupatorium rotundifolium L.
Cercospora ageratoides Ell. & Ev.
Eupatorium urticaefolium L.
Cercospora ageratoides Ell. & Ev.
Ficus carica L.
Cercospora bolleana (Thüm.) Speg.
Fraxinus sp.?
Cercospora superflua Ell. & Holw.
Fraxinus excelsior L.
Cercospora fraxini (DC.) Sacc.
Garrya elliptica Dougl.
Cercospora glomerata Hark.
Gaultheria procumbens L.
Cercospora gaultheriae Ell. & Ev.
Gleditsia triacanthos L.
Cercospora condensata Ell. & Kell.
Cercospora olivacea (B. & Rav.) Ell.
Gymnocladus dioica (L.) Koch
Cercospora gymnocladii Ell. & Kell.
Helianthemum sp.
Cercospora helianthami Br. & Cav.
Helianthemum polifolium roseum Willk.
Cercospora helianthemi Br. & Cav.
Heuchera sp.
Cercospora heucherae Ell. & Mart
Heuchera americana L.
Cercospora heucherae Ell. & Mart.
Ilex glabra (L.) Gray
Cercospora ilicis Ell.
Impatiens noli-tangere L.
Cercospora campi-silii Speg.
Ipomoea hederacea L.
Cercospora ipomoeae Wint.
Ipomoea lacunosa L.
Cercospora ipomoeae Wint.
Ipomoea pandurata C. F. W. May
Cercospora ipomoeae Wint.
Ipomoea purpurea Lam.
Cercospora ipomoeae Wint.
Leucospermum conocarpum R. Br.
Cercospora protearum Cooke
Linum virginianum L.
Cercospora lini Ell. & Ev.
Lippia lanceolata Michx.
Cercospora lippiae Ell. & Ev.
Lippia nodiflora Michx.
Cercospora lippiae Ell. & Ev.
Lobelia cardinalis L.
Cercospora lobeliaecola Solheim
Lupinus diffusus Nutt.
Cercospora lupini Cooke
Lysimachia stricta Ait.
Cercospora lysimachiae Ell. & Hal.
Magnolia glauca L.
Cercospora magnoliae Ell. & Hark.
Maianthemum convallaria Web.
Cercospora maianthemii Fckl.
Malva rotundifolia L.
Cercospora malvarum Sacc.
Melilotus alba Desr.
Cercospora davisii Ell. & Ev.
Menispermum canadense L.
Cercospora meninspermi Ell. & Holw.
Osmorrhiza longistylis (Torr.) DC.
Cercospora osmorrhizae Ell. & Ev.
Parthenocissus sp.
Cercospora ampelopsidis Peck
Parthenocissus quinquefolia Planch.
Cercospora ampelopsidis Peck
Parthenocissus quinquefolia hirsuta Planch.
Cercospora ampelopsidis Peck
Passiflora lutea L.
Cercospora fusco-virens Sacc.
Pastinaca sativa L.
Cercospora pastinacae (Sacc.) Peck
Cercospora pastinacina Solheim
Petroselinum hortense Hoffm.
Cercospora petroselini Sacc.
Phaseolus sp.
Cercospora cruenta Sacc.
Phaseolus lunatus L.
Cercospora canescens Ell. & Mart.
Philadelphus coronarius L.
Cercospora angulata Wint.
Physalis virginiana Mill.
Cercospora physalidis Ell.
Piper sp.
Cercospora portoricensis Earle
Piper aduncum L.
Cercospora portoricensis Earle
Piper hispidum Sw.
Cercospora portoricensis Earle
Piper peltatum L.
Cercospora portoricensis Earle

- Piper umbellatum* L.
Cercospora portoricensis Earle
Platanus occidentalis L.
Cercospora platanicola Ell. & Ev.
Polygonum sp.
Didymaria effusa (B. & C.) Solheim
Polygonum acre HBK.
Didymaria effusa (B. & C.) Solheim
Polygonum hydropiper L.
Didymaria effusa (B. & C.) Solheim
Polygonum hydropiperoides Michx.
Didymaria effusa (B. & C.) Solheim
Polygonum pennsylvanicum L.
Didymaria effusa (B. & C.) Solheim
Prunus virginiana L.
Cercospora cerasella Sacc.
Ranunculus sp.
Didymaria didyma (Ung.) Schroet.
Ranunculus "acer"
Didymaria didyma (Ung.) Schroet.
Ranunculus lanuginosus L.
Didymaria didyma (Ung.) Schroet.
Ranunculus lingua L.
Didymaria didyma (Ung.) Schroet.
Ranunculus nemorosus DC.
Didymaria didyma (Ung.) Schroet.
Ranunculus pennsylvanicus L.
Didymaria didyma (Ung.) Schroet.
Ranunculus polyanthemus L.
Didymaria didyma (Ung.) Schroet.
Ranunculus repens L.
Didymaria didyma (Ung.) Schroet.
Ranunculus septentrionalis Poir.
Didymaria didyma (Ung.) Schroet.
Raphanus sativus L.
Cercospora atrogrisea Ell. & Ev.
Reseda odorata L.
Cercospora resedae Fckl.
Rhus sp.
Cercospora rhoina Cooke & Ell.
Rhus canadensis Marsh.
Cercospora rhoina Cooke & Ell.
Rhus copallina L.
Cercospora rhoina Cooke & Ell.
Rhus glabra L.
Cercospora rhoina Cooke & Ell.
Rhus pumila Michx.
Cercospora rhoina Cooke & Ell.
Rhus toxicodendron L.
Cercospora rhoina Cooke & Ell.
Cercospora toxicodendri Ell.
Rhus typhina L.
Cercospora rhoina Cooke & Ell.
Rhus vernix L.
Cercospora rhoina Cooke & Ell.
Ribes sanguineum Pursh
Cercospora ribicola Ell. & Ev.
Rosa blanda Ait.
Cercospora rosaecola Pass.
Rosa canina L.
Cercospora hypophylla Cav.
Rubus trivialis Michx.
Cercospora rubi Sacc.
Ruellia ciliosa Pursh
Cercospora consociata Wint.
Sagittaria latifolia Willd.
Cercospora sagittariae Ell. & Kell.
Sambucus nigra L.
Cercospora depazeoides (Desm.) Sacc.
Cercospora ticinensis Br. & Cav.
Sambucus racemosa L.
Cercospora lateritia Ell. & Hal.
Sicyos angulatus L.
Cercospora echinocystis Ell. & Mart.
Silphium integrifolium Michx.
Cercospora silphii Ell. & Ev.
Smilax sp.
Cercospora petersii (B. & C.) Atk.
Smilax aspera L.
Cercospora smilacina Sacc.
Smilax glauca Walt.
Cercospora petersii (B. & C.) Atk.
Smilax hispida Muhl.
Cercospora petersii (B. & C.) Atk.
Smilax laurifolia L.
Cercospora petersii (B. & C.) Atk.
Smilax mauritanica L.
Cercospora smilacis Thüm.
Smilax rotundifolia L.
Cercospora petersii (B. & C.) Atk.
Smilax tamnoides Gray (5th ed. of Man.)
Cercospora petersii (B. & C.) Atk.
Solanum tuberosum L.
Cercospora concors (Casp.) Sacc.
Solidago sp.
Cercospora cana Sacc.
Solidago canadensis L.
Cercospora cana Sacc.
Sorghum halapense (L.) Pers.
Cercospora sorghi Ell. & Ev.
Sorghum vulgare Pers.
Cercospora sorghi Ell. & Ev.
Tecoma radicans Juss.
Cercospora sordida Sacc.

- Teucrium canadense* L.
 Cercospora teucrii Ell. & Kell.
- Thalictrum flavum* L.
 Cercospora thalictri Thüm.
- Tilia europaea* L.
 Cercospora microsora Sacc.
- Trigonella foenum-graceum* L.
 Cercospora radiata Fckl.
- Vernonia baldwinii* Torr.
 Cercospora oculata Ell. & Kell.
 Cercospora vernoniae Ell. & Kell.
- Vicia faba* L.
 Cercospora zonata Wint.
- Viola cucullata* Ait.
 Cercospora granuliformis Ell. & Holw.
- Viola tricolor* L.
 Cercospora violae-tricoloris Br. & Cav.
- Vitis* sp.
 Cercospora viticola (Ces.) Sacc.
- Zea mays* L.
 Cercospora sorghi El. & Ev.
- Zinnia pauciflora* L.
 Cercospora zinniae Ell. & Mart.

SPECIES INDEX

(Synonymous names are in italics.)

The genus is *Cercospora* unless otherwise designated.

- absinthii* (Peck) Sacc., 61, 62
absinthium Peck, *Helminthosporium*, 61
acalyphae Peck, 10, 12, 16, 31
acerina Hart., 60
acnidae Ell. & Ev., 32
acromiae Stevenson, 56
agerati Stev., 63
ageratoides Ell. & Ev., 32
alismatis Ell. & Ev., 32
alternantherae Ell. & Lang., 33
althaeina Sacc., 12
amorphophali Henn., 63
ampelopsidis Peck, 13, 15, 57, 58
angulata Wint., 38
apii Fresen., 7, 10, 12, 15, 16, 17, 25, 34, 35, 44, 45, 46
apii Fresen. var. *carotae* Pass., 43
apii Fresen. var. *pastinacae* Sacc., 44, 45
apii Fresen. var. *petroselinii* Sacc., 40
arctii Stev., 38
atrogrisea Ell. & Ev., 35

beticola Sacc., 12, 16, 17, 22, 23, 39
bolleana (Thüm.) Speg., 12, 17, 41
brassicae (Berk.) Sacc., *Alternaria*, 19
brunkii Ell. & Galw., 12
bupleuri Pass., 30

campi-silii Speg., 46
cana Sacc., 42, 43
cana (Sacc.) Sacc., *Cercospora*, 42, 43
canescens Ell. & Mart., 39
canum Pass., *Fusidium*, 42, 43
carica Stev. & Hall, *Colletotrichum*, 19
carotae (Pass.) Solheim, 11, 43
catenospora Atk., 12
caulicola Wint., 16
cercidicola Ell., 10, 11, 12, 23, 47
cercidicola Ell. var. *cornioides* Tehon, 47
cerasella Sacc., 17, 41
clavata (Ger.) Peck., 39, 53
clavatum (Ger.) Cooke, *Virgasperium*, 7
coffeicola Berk. & Cooke, 16
concors (Casp.) Sacc., 12, 62
condensata Ell. & Kell., 10, 54
condensata Ell. & Kell. var. *desmanthii* Ell. & Kell., 29
consociata Wint., 51
copallina Cooke, 49, 50
cruetna Sacc., 39

davisii Ell. & Ev., 35
demetritioniana Wint., 36

depazeoides (Desm.) Sacc., 39
desmanthii Ell. & Kell., 29
desmodii Ell. & Kell., 41
destructiva Rav., 31
didyma (Ung.) Schroet., *Didymaria*, 20, 64, 65
didyma Ung., *Ramularia*, 20, 64, 65
dubia (Riess) Wint., 46
duplicata Ell. & Ev., 60

echinocystis Ell. & Mart., 36, 37
effusa (B. & C.) Solheim, *Didymaria*, 20, 64, 65
effusa B. & C., *Cladosporium*, 65, 67
effusa (B. & C.) Ell., 64

ferruginea Fckl., 10, 11, 12, 23, 61
fraxini (DC.) Sacc., 29
fructi Stev. & Hall, *Volutella*, 18
fusca Rand, 12
fusco-virens Sacc., 53

gaultheriae, Ell. & Ev., 28
glauescens Wint., 30
glomerata Hark., 58
granuliformis Ell. & Holw., 46
gymnocladii Ell. & Kell., 56

helianthemi Bri. & Cav., 53
heucherae Ell. & Mart., 48
hydropiperis (Thüm.) Speg., 64, 66, 67
hydropiperis Thüm., *Helminthosporium*, 66, 67
hypophylla Cav., 31

ilicis Ell., 53
illinoensis Barth., 12, 13, 14, 15, 19, 23, 52, 53
ipomoeae Wint., 37

lateritia Ell. & Hal., 52
lini Ell. & Ev., 60
lippiae Ell. & Ev., 38
lobeliaecola Solheim, 64
lupini Cooke, 52
lysimachiae Ell. & Hals., 27
lythracearum Heald & Wolf, 12, 16, 17

maculata Willd., *Medicago*, 16
maculatum Cooke, *Virgasperium*, 7
magnoliae Ell. & Hark., 40
maianthemi Fckl., 46
malvarum Sacc., 39
medicaginis Ell. & Ev., 12, 16, 17
menispermii Ell. & Holw., 62

- microsora* Sacc., 12, 17, 39
mississippiensis Tracy & Earle, 55
niger, van Tieg., *Aspergillus*, 18
occidentalis Cooke, 28
oculata Ell. & Kell., 39
olivacea (B. & R.) Ell., 58
osmorrhizae Ell. & Ev., 47
passaloroides Wint., 62
pastinacae (Sacc.) Peck, 12, 44, 45, 46
pastinacae Karst., *Cercospora*, 45
pastinacina Solheim, 45, 46
personata (B. & C.) Ell., 12, 17, 29
petersii (B. & C.) Atk., 10, 11, 28, 48, 51, 54
petersii B. & C., *Helminthosporium*, 54, 55
petroselinii Sacc., 40
physalidis Ell., 39
pipericola Sacc. & Syd., 62
piperis Ell. & Ev., 62, 63
piperis Pat., 63
platanicola Ell. & Ev., 31
polygonorum Cooke, 65, 67
portoricensis Earle, 10, 11, 62, 63
protearum Cooke, 31
pusilla Ung., *Ramularia*, 20
pustula Cooke, 57, 58
radiata Fckl., 39
radicicola Woll., *Fusarium*, 18
resedae Fckl., 39
rhoina Cooke & Ell., 49, 50
ribicola Ell. & Ev., 50
rosaecola Pass., 41
rubi Sacc., 57
sagittariae Ell. & Kell., 39
silphii Ell. & Ev., 56
simulata Ell. & Ev., 41
smilacina Sacc., 10, 12, 27, 28, 54, 55
smilacis Thüm., 16, 28, 50, 51, 54, 55
sordida Sacc., 16, 59
sorghii Ell. & Ev., 57
squalidula Peck, 39
superflua Ell. & Holw., 41
teucriti Ell. & Kell., 39
thalictri Thüm., 58
ticinensis Br. & Cav., 28
toxicodendri Ell., 47
tuberosa Ell. & Kell., 10, 30
tulasnei Sacc., *Ramularia*, 20
umbrata Ell. & Holw., 42
ungeri Corda, *Didymaria* 20, 64, 65
vernoniae Ell. & Kell., 28
violae-tricoloris Br. & Cav., 40
viticola (Ces.) Sacc., 29
zinniae Ell. & Mart., 28
zonata Wint., 29

LIST OF NEW NAMES AND NEW COMBINATIONS

<i>Cercospora</i> carotae (Passerini) Solheim, n. sp.	43
<i>Cercospora</i> pastinacina Solheim, n. name and n. comb.	45
<i>Cercospora</i> lobeliaecola Solheim, n. name	64
<i>Didymaria</i> (Corda) <i>emend.</i> Solheim	64
<i>Didymaria</i> effusa (Berkeley and Curtis) Solheim, n. comb	65

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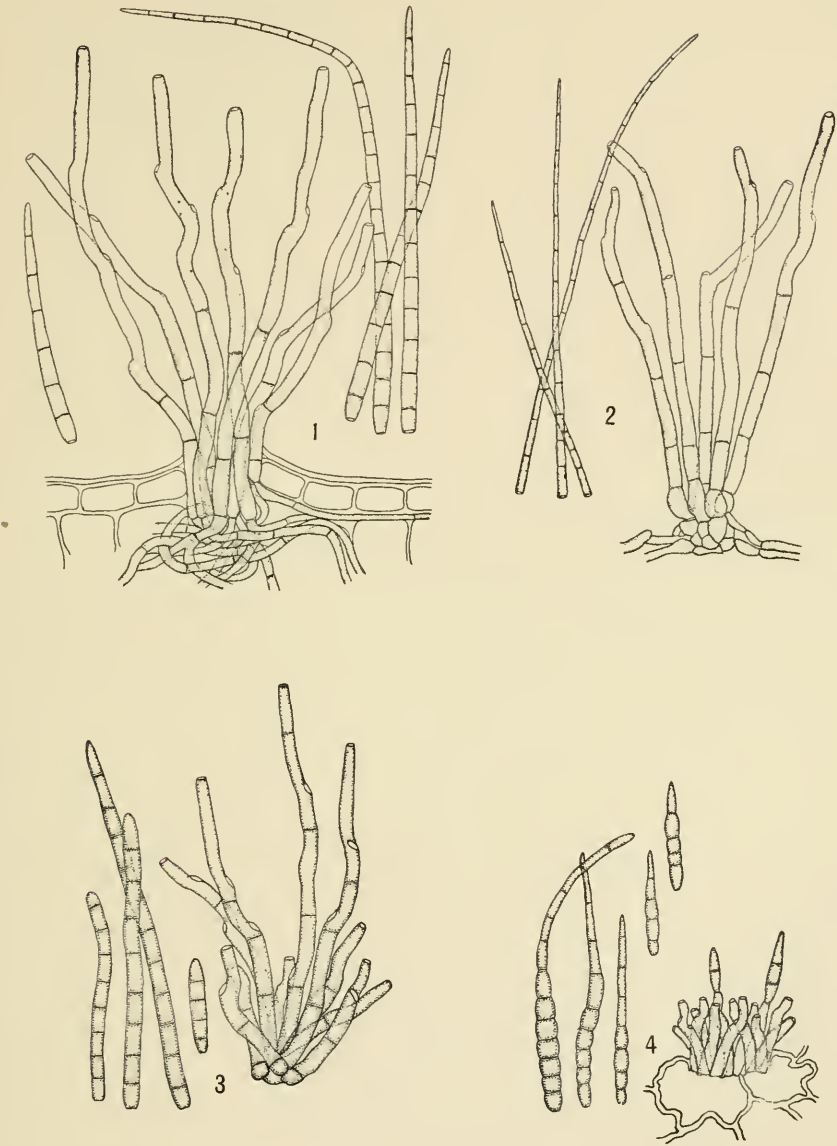
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PLATE I

EXPLANATION OF PLATE I

- FIG. 1. *Cercospora apii* Fresen., conidiophores simple, loosely stromatic; conidia acicular to acicular-obclavate.
- FIG. 2. *Cercospora acalyphae* Peck, conidiophores simple, loosely stromatic; conidia acicular.
- FIG. 3. *Cercospora althacina* Sacc., conidiophores simple; conidia cylindrical.
- FIG. 4. *Cercospora gymnocladii* Ell. & Kell., conidiophores simple; conidia abruptly obclavate.



SOLHEIM

CERCOSPORA

PLATE I

PLATE II

EXPLANATION OF PLATE II

- FIG. 5. *Cercospora cercidicola* Ell., conidiophores coremioid, with opposite branching, loosely stromatic; conidia abruptly obclavate.
- FIG. 6. *Cercospora ferruginea* Fckl., conidiophores with alternate branching, non-stromatic; conidia abruptly obclavate.
- FIG. 7. *Cercospora resedae* Fckl., conidiophores simple; conidia acicular.
- FIG. 8. *Cercospora illinoensis* Barth., conidiophores with opposite and alternate branching, substromatic; conidia cylindrical.

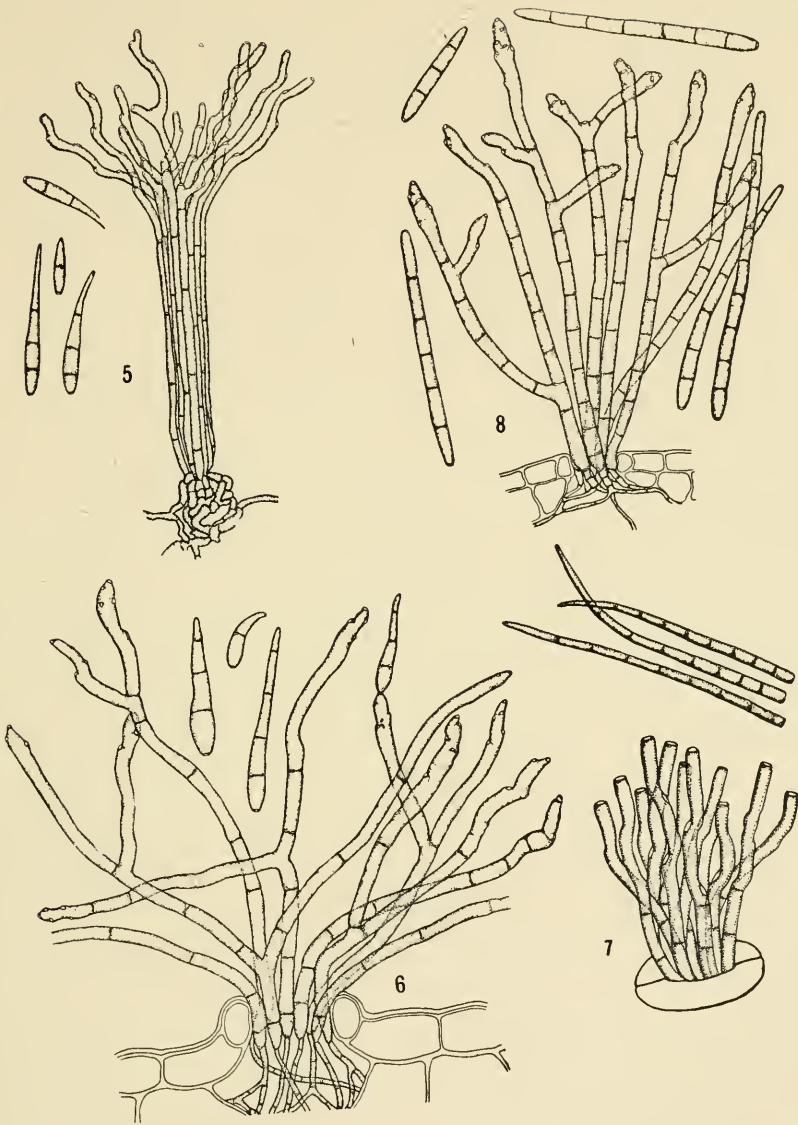


PLATE III

EXPLANATION OF PLATE III

- FIG. 9. *Cercospora smilacis* Thüm., conidiophores with alternate branching, arising from a tuberculate stroma; conidia cylindrical.
- FIG. 10. *Cercospora smilacina* Sacc., conidiophores simple, arising from a tuberculate stroma; conidia acicular-obclavate.
- FIG. 11. *Cercospora petersii* (B. & C.) Atk., conidiophores simple, more or less coremioid, arising from a tuberculate stroma; conidia abruptly obclavate.
- FIG. 12. *Cercospora tuberosa* Ell. & Kell., conidiophores simple, arising from a tuberculate stroma; conidia cylindrical.

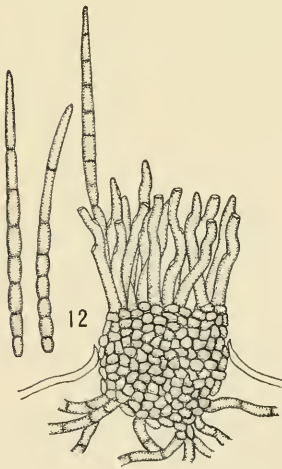
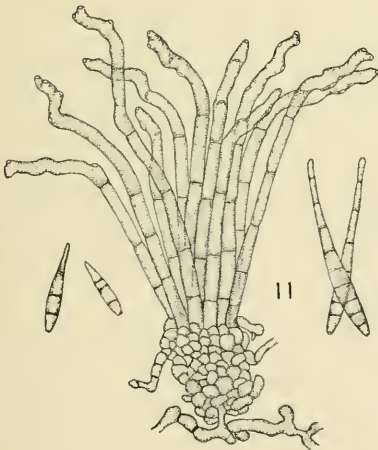
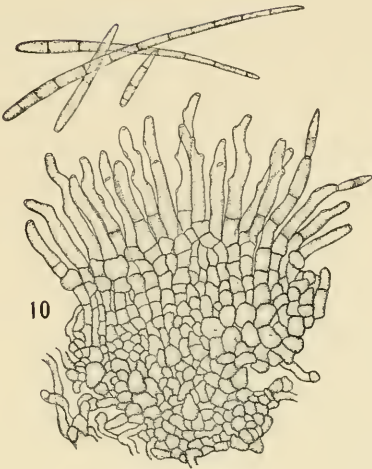
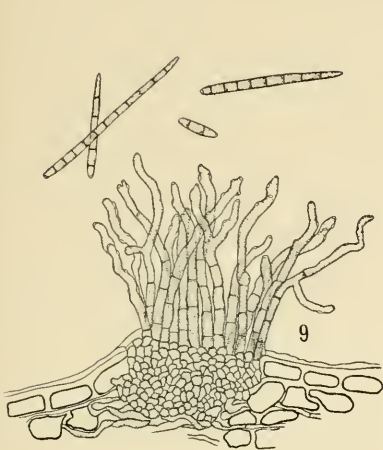
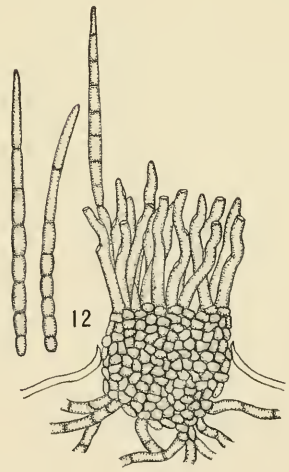
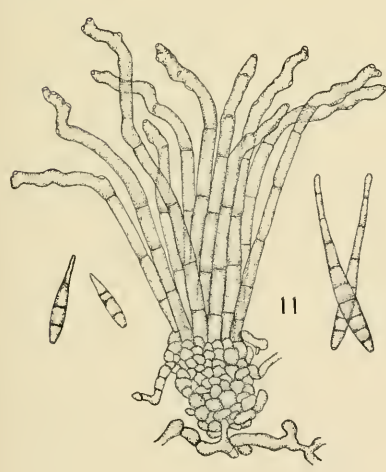
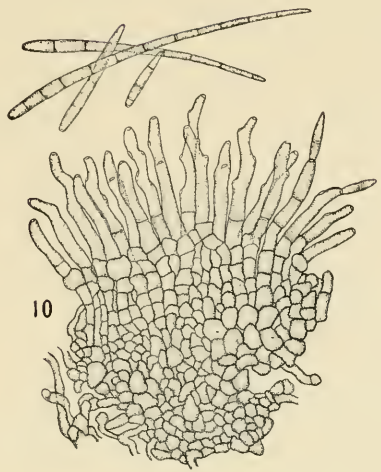
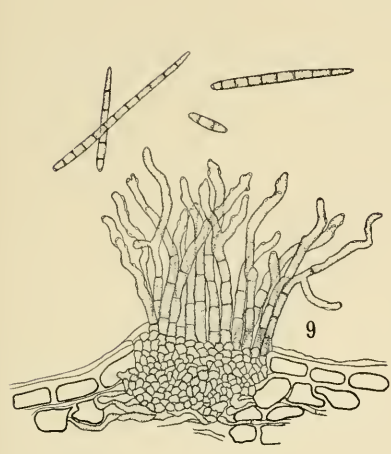


PLATE IV

EXPLANATION OF PLATE IV

- FIG. 13. *Cercospora portoricensis* Earle, external mycelium arising from the conidiophores; conidiophores with alternate branching, arising from the internal mycelium or effused on the external mycelium; conidia cylindrical.
- FIG. 14. *Cercospora pastinacae* (Sacc.) Peck, conidiophores simple, substromatic; conidia fusiform.
- FIG. 15. *Didymaria effusa* (B. & C.) Solheim, conidiophores simple; conidia clavate.
- FIG. 16. *Didymaria didyma* (Ung.) Schroet., conidiophores simple, substromatic; conidia clavate.



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MORPHOLOGY, TAXONOMY, AND
BIOLOGY OF LARVAL
SCARABAEOIDEA

WITH FIFTEEN PLATES

BY

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Contribution No. 137 from the Entomological Laboratories of the
University of Illinois

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TABLE OF CONTENTS

Introduction.....	7
Economic importance.....	8
Historical review.....	10
Taxonomic literature.....	11
Biological and ecological literature.....	12
Materials and methods.....	13
Acknowledgments.....	15
Morphology.....	16
The head and its appendages.....	17
Antennae.....	18
Clypeus and labrum.....	20
Epipharynx.....	22
Mandibles.....	33
Maxillae.....	37
Hypopharynx.....	39
Labium.....	40
Thorax and abdomen.....	40
Segmentation.....	40
Setation.....	41
Radula.....	41
Legs.....	42
Spiracles.....	43
Anal orifice.....	43
Organs of stridulation.....	44
Postembryonic development and biology of the Scarabaeidae.....	47
Eggs.....	47
Oviposition preferences.....	47
Description and length of egg stage.....	48
Egg burster and hatching.....	48
Larval development.....	50
Molting.....	50
Postembryonic changes.....	54
Food habits.....	54
Relative abundance.....	58
Hibernation.....	61
Pupation.....	63
Length of life cycle.....	64
Melolonthinae.....	64
Rutelinae.....	66
Dynastinae.....	67
Cetoniinae.....	70
Laparosticti.....	71
Taxonomy.....	72
Keys.....	73
Summary.....	81
Bibliography.....	82
Explanation of plates.....	85
Index.....	115

INTRODUCTION

The larvae of the superfamily Scarabaeoidea are commonly called white grubs or grubworms. Forbes, writing in 1891 on insects of this group in relation to their life histories, said that "it is necessary that the observer should learn to distinguish species of these insects in the grub and larval stage." Among the numerous genera, the species of which are usually more readily recognized in the adult form, there are many species that are almost indistinguishable from one another in the larval stage. To identify them it is usually necessary to rear the specimens. This requires a long period of time and often involves dangers of loss from one cause or another during the period of rearing. In a number of groups, especially in the subfamily Melolonthinae, the life-cycle covers a period of from two to three years, and in northern latitudes even four years. Such a long larval stage makes rearing difficult. Moreover, since the larval life is spent under the surface of the soil, it is difficult to maintain rearing conditions as near normal as necessary. Not only do the representatives of the various subfamilies differ in length of life in various localities, but they may exhibit wide degrees of variance even in the same localities.

Rapid strides have been made in our knowledge of the life histories of these insects within the last twelve years (1917-29), and it is becoming increasingly more important, as we survey the great differences exhibited, that we be able to recognize the larval forms. As with all other groups of insects, our knowledge of the developmental stages lags behind our knowledge of the adults. This is especially true in the fields of morphology and taxonomy and to a lesser extent in the field of biology. Prior to the studies by Davis and others, which have materially increased our knowledge of the group, most of our knowledge of the biology of these insects has been based on fragmentary accounts scattered in the literature. The present work deals with morphological, taxonomic, and biological studies of the various species of white grubs. The morphological studies have aided materially in constructing the diagnostic keys to the various genera which are included. Life-history studies made by the writer, some of which have, in part, appeared in different publications, are here brought together and briefly summarized to make the present work as nearly a complete unit as possible.

ECONOMIC IMPORTANCE

Of the four families, Passalidae, Lucanidae, Scarabaeidae, and Trogidae, comprising the superfamily Scarabaeoidea (or Lamellicornia), the family Scarabaeidae is the best known and most important. The others have only slight economic importance.

The family Passalidae, which inhabits decaying wood, is represented in tropical forests by numerous species but in North America by only one species, *Passalus cornutus* Fab. Some species of this family are of biological interest because of a certain degree of social organization ascribed to them, the adults being known to attend the larvae and care for them throughout their period of development to maturity. The adults chew the woody food and prepare it before feeding it to the larvae. The hastening of decay in rotten logs can be said to be a beneficial phase exhibited by this group of insects.

The Lucanidae, or stag-beetles, exhibit wide sexual differences in the adult stage. Their larvae, like the Passalidae, live in rotten logs or roots. About 300 species of Lucanidae occur throughout the world, but only 30 species are recorded by Leng (1920) from North America. Aside from their biological interest, the unique stridulation structures of the larvae and the benefits incurred from the hastening of decay, the family can be considered of little importance.

The family Trogidae is one of our newer families, having recently been raised to its present position from subfamily rank in the Scarabaeidae. Of the genera occurring in North America, the genus *Trox* is the most important. The larvae of *Trox* are scavengers and are usually found in dried, decomposing, animal matter or on the soil under such matter. Little is known of their life history.

The Scarabaeidae in the adult stages are known as chafers, May beetles, June bugs, dung beetles, and dor beetles. They constitute a large family with about 14,000 species known from all parts of the world. The family is divided into two categories, or groups, the Laparosticti and the Pleurosticti. The Laparosticti are, for the most part, coprophagous in habits. The Coprinae, Aphodinae, and Geotrupinae are the better known subfamilies with coprophagous habits. A few of the Coprinae are known to be myrmecophilous and live as symphiles in the nests of ants. The coprophagous habit is, by far, the most important. The group Pleurosticti contains a large number of important economic insects. These occur in four subfamilies: the Melolonthinae, the Rutelinae, the Dynastinae, and the Cetoniinae.

The larvae of the subfamilies here considered are recognized in many parts of the world as pests of planted crops and are almost universally known as "white grubs." One of the most notorious members of the group is the European "Hanneton," *Melolontha melolontha*, which has been

known for over a century as a destructive enemy of the roots of crops. It belongs to the subfamily Melolonthinae, to which our common American species of May beetles, or June bugs, are assigned. Certain species of Phyllophaga (Lachnosterna), both adults and larvae, are perhaps the most destructive members of the family in North America, and their injury is too well known to require extended discussion.

In some of the states west of the Mississippi the greatest loss from white grubs occurs where the larvae of *P. lanceolata* (Say) attack the roots of wheat and often destroy thousands of acres in a single season. Considering the country as a whole, most of the principal crops as well as native prairie pastures, meadows, and lawns have suffered injury from various species. In some localities gardens suffer. Potatoes especially have paid a heavy toll in the last few years. Strawberry beds have been the object of regular attacks, and ornamentals of all kinds, particularly those recently set out, have been seriously damaged. Many lawns have been killed by the grubs, and serious loss has occurred in the bluegrass pastures. According to Davis (1918), alfalfa is usually considered free from injury, but it has been found damaged in a number of localities. In attacking this crop, the grub enters the tap-root an inch or two below the surface of the soil, excavates a cavity, and burrows upward and downward in much the same manner as some of the root-boring insects.

Among the Rutelinae, two species, *Pelidnota punctata* L. and *Cotalpa lanigera* (L.) are notably injurious in the United States. The damage caused by the spotted grapeleaf beetle, *Pelidnota punctata*, to the foliage of grapes during some years attracts considerable attention, but the larvae, living in rotten wood, such as logs and old stumps, can be regarded as beneficial because their activities in these situations hasten decay. The goldsmith beetle, *Cotalpa lanigera*, has been reported by Davis (1916) as ranking next in importance to the species of Phyllophaga. He says that the grubs in Michigan are destructive to raspberry bushes, strawberries, corn, and grass. Other native species of Rutelinae treated here are not of so much economic importance, but *Anomala innuba* at times becomes numerous. The beetles of this species do some damage to the kernels of growing wheat, which they attack while "in the milk," and the grubs feed on the roots of various plants. Two important imported members of this subfamily are the Japanese beetle, *Popillia japonica* Newm., and the Asiatic beetle, *Anomala orientalis* (Waterhouse).

Among the representatives of the Dynastinae dealt with herein, *Ligyroides relictus* Say is not known to be a crop pest, but a near relative, *Ligyroides gibbosus* DeGeer, is an important enemy of carrots and domesticated sunflower crops, and is known as the carrot beetle.

The best known American species of the Cetoniinae are the bumble flower beetle, *Euphoria inda* L., and the green June beetle, also called the

fig eater, *Cotinis (Allorhina) nitida* L. The bumble flower beetle is a somewhat general feeder, being found upon flowers, eating the pollen, and upon corn stalks where it feeds on the green cob by sucking the juices. It also occurs on peaches, grapes, and apples, and occasionally its injury becomes serious. The larva is not known to cause damage. The green June beetle, on the other hand, is a pest in the grub stage, feeding upon the roots of grasses and often doing immense damage to tobacco plantings, lawns, and golf courses (Chittenden and Fink, 1922). Two species of Euphoria, *E. sepulchralis* Fab. and *E. fulgida* Fab., are neither of great importance economically. They feed in the adult stage on the pollen and nectar of flowers. The beetles of *E. sepulchralis* feed on the tips of ears of corn, making way for further injury by the green June beetle, *Cotinis nitida*. The species of *Osmoderma* pass their developmental periods in decaying wood, as do also the larvae of *Trichiotinus* (*Trichius*), and are only of minor significance.

HISTORICAL REVIEW

Some members of the families Scarabaeidae and Lucanidae have been known from ancient times. The Romans frequently hung the mandibles of Lucanus on the necks of children or wore them in the form of amulets to ward off disease. In Germany, Lucanus was known as the "fire-starter" because it was said to carry live coals into houses with its pinchers, thereby starting conflagrations. The people would often cooperate in their efforts to drive them away. The sacred beetle of Egypt has made the family Scarabaeidae renowned, and many interesting tales and superstitions have been connected with it. These myths and legends are too numerous to be discussed here and, except for historical value, are irrelevant in a work of this nature.

The meaning and origin of the word Scarabaeus is clouded in doubt and uncertainty. Papis, a grammarian of the eleventh century, says the word comes from *cabus* or *caballus*, meaning horse, because the insects according to the ideas of the times were thought to be born from the cadaver of a horse. Bochart derives the word from *chapphas*, which signifies an excavator, in view of the characteristic action of coprophagous species. Fabricius derives it from the Greek *to dig*, and MacLeay from the Greek *to scratch* or *scrape*. Mulsant, Martini, and others accept Aristotle's interpretation, which derives it from a Greek word signifying an insect that is unknown to us.

The first splitting of the group, as defined by Linnaeus, occurred when Scopoli (1763) separated the genus Lucanus from Scarabaeus. Fabricius, Olivier, and others followed with many new genera, until ultimately the two groups represented by Scarabaeus and Lucanus were elevated to family rank under the superordinal appellation Lamellicornia, a term which was first used either by Lamark (1817) or Latreille (1817). According to

Burmeister, it is not known which of the two was the originator of the term, but it is generally attributed to Latreille, to whom is also credited the origin of our modern conception of the family group. The termination *-idae* was for the first time generalized in entomology by MacLeay in 1819. Leng (1920) in his recent check list of North American Coleoptera considers the Lamellicornia under the superorder Scarabaeoidea, recognizing three families, Scarabaeidae, Lucanidae, and Passalidae. The recent supplement to Leng's list, by Leng and Mutchler (1927), considers the subfamily Troginae as of family rank, so that as now constituted there are four recognized North American families, namely, Scarabaeidae, Lucanidae, Passalidae, and Trogidae.

There have been several European attempts to work out the classification of larval stages of the Scarabaeoidea. The anatomical descriptions of individual species are fairly numerous in scattered foreign works, but the problem in America has been given little attention. Until recently there has been no attempt at a general classification, and isolated descriptions are scarce and in many instances inadequate.

TAXONOMIC LITERATURE

A study of the distinguishing characters of American lamellicorn larvae has been a long-felt need. Moreover, their economic importance makes such a study of extreme value. It is highly desirable to be able to recognize the different genera at least, and, when possible, the species belonging to the genera. Forbes (1894) in his Eighteenth Report (p. 97) stated that "life-histories are not sufficiently different to make discrimination of species a matter of practical importance, and for economic purposes, consequently, the white grubs may usually be classed as one." A little later in the same report (footnote, p. 105), in speaking of the verification of life-histories, he says "it is necessary that the observer should learn to distinguish species or at least groups of species of these insects in the grub and larval stage." Forbes then pointed out differences between *Ochrosidia* (*Cyclocephala*) and *Phyllophaga* (*Lachnosterna*) grubs. The latter genus was divided into three groups: the *hirticula-rugosa*, *fusca-inversa*, and *gibbosa* (now *futilis*) group. Except for the work of Forbes and scattered isolated descriptions, no attempt was made in this country to characterize the various groups of the family until Böving (1921) published a short key dealing with several allied genera of the green Japanese beetle (*Popillia japonica*), which is based in part on the work of Schiödte (1874). This generic key indicated the distinguishing characters of one European and five American genera.

In contrast to the work done in America on this group, a number of European papers are available which, although dealing with but few genera occurring in this country, are of value in a study of this nature.

Chapuis and Candeze (1855, p. 452) noted that the habits and metamorphosis of no group of European beetle larvae were as well known as the lamellicorns. The first to attempt a classification of these larvae was DeHaan (1836), who used both external and internal characters to distinguish eight genera. DeHann made use of the malpighian tubules, and in his work the drawings of the alimentary canal are especially good. The next attempt at classification was made by Mulsant (1842), who compiled a key based on external characters alone. The same year (1842) Burmeister published in a large measure the groupings of DeHann. Erichson (1848) presented a study of the group and used an arrangement of the families, which we now recognize as subfamilies. Erichson's key is also found in the catalogue of coleopterous larvae in which Chapuis and Candeze in 1855 brought together the references to descriptions of larvae known at that time. Schiödte's classical work on the larvae of Coleoptera appeared in 1874 in several parts, of which Part VIII deals with the lamellicorn larvae. The drawings in this work are indeed excellent. Three years later Perris (1877) published his well-known work which contains the most complete key to genera that we have. He added many new descriptions of lamellicorn larvae. Recently Ritterschus (1927) has described somewhat completely the morphological details of *Anomala aenea* Geer and *Phyllopertha horticola* L. This work is perhaps the first to give any detailed consideration to the epipharynx of white grubs. More will be said concerning this work later. A recent paper by the writer (1928) on the epipharynx of the larvae contains a preliminary generic key, including a few species, based in great part on characters of the epipharynx. This key with corrections, additions, and emendations is used in the present work as a basis of generic distinction.

BIOLOGICAL AND ECOLOGICAL LITERATURE

In America the life-cycles of the Lucanidae and Passalidae are little known and not thoroughly worked out. The Trogidae are as yet untouched. The economic species of the Scarabaeidae have, in recent years, become better known, although scarcely anything has been done on the coprophagous forms. Previous to 1916, our knowledge of the life-cycles of the American species of *Phyllophaga* was confined to the work of Chittenden (1899) who reared a single specimen of *P. fervida* (*arcuata*) and to those of Davis (1913) who reported a two-year life-cycle for *P. tristis*. In 1916, Davis discussed the length of life of 18 species of the genus, but did not determine the length of the various stages. This work is of great importance to our knowledge of the group. Smyth (1917) published the results of life-history studies of certain Porto Rican species of *Phyllophaga*, in which our first account is available concerning the length of the various instars.

The writer has from time to time published life-history studies of various species of the family. The life-cycle of *P. lanceolata* was noted as having a

two-year period of development with quite varied habits from the majority of species of Phyllophaga. In another paper (1920) seven species, *futilis*, *rubiginosa*, *vehemens*, *crassissima*, *rugosa*, *implicata*, and *submucida* of the same genus were reported as having a two-year or a three-year life-cycle. This was followed by a more comprehensive report (1925) of the studies made on ten other species of Phyllophaga and some other members of the family belonging to different subfamilies. Along with these were recorded data on the development of three species of Rutelinae, one Dynastinae, and two Cetoniinae. In the present work these studies will be brought together for the purpose of comparison.

In the subfamily Rutelinae the species of the tribe Anomalini require one year for completion of their life-cycle. *Anomala binotata* and *A. innuba* were found by the writer (1918 and 1925) to have a one-year period. The same time is required for *Strigoderma arboricola* (Hayes, 1921). The Oriental *Anomala* and the Japanese beetle are likewise known to have a one-year life-cycle. In the tribe Rutelini, of the subfamily Rutelinae, the life-history is longer. It has been shown (Hayes, 1925) that *Pelidnota punctata* requires two years to mature and *Cotalpa lanigera* needs either two or three years.

All the species of the Dynastinae so far studied by the writer and by others require but a single year to develop, with the exception of *Strategus quadrifoviatu*s (Smyth, 1916) which requires more than one year but considerably less than two years. The species of the subfamily Cetoniinae, as far as known, usually occupy one year in the completion of growth. *Cotinus nitida* requires one year (Chittenden and Fink, 1922) while the writer (1925) recorded the same length of life for *Euphoria fulgida* and *E. sepulchralis*.

MATERIALS AND METHODS

The methods of study for the data herein reported are of two distinct types, biological and morphological. The biological end of the problem demanded rearing methods which enabled the handling of the immature stages over a long period of time; while the morphological studies, made primarily for taxonomic results, required the collection and preservation of definitely known larvae and some slight laboratory technique.

On account of their subterranean habits and long period of development, white grubs are difficult to rear to the adult stage. The difficulty arises not only from their prolonged life-cycle, but also because of the many parasitic fungi and other diseases attacking the grubs while being reared under artificial conditions. In order to be sure of having some specimens mature, it was necessary to handle large numbers of eggs and larvae; and in order to study molting, it was necessary to keep them isolated. Davis (1915) and Smyth (1917) have devised methods of rearing white grubs and May beetles, and suggestions of these two writers were fol-

lowed in this work. These methods with some others are here briefly summarized.

To procure eggs it was only necessary to confine the beetles over a few inches of damp, well-packed soil. Any sort of cage could be used, but most of them were one-gallon tins, half-filled with moist earth, the tops being perforated. The leaves of various trees were frequently supplied for food by merely placing them on the surface of the soil. The earth was sifted or carefully gone over for eggs every second day. It was found that disturbing the soil every day produced a tendency for the beetles to lay fewer eggs. The eggs were transferred to individual cavities in closely packed, dampened soil in one-ounce or two-ounce tin salve boxes, where they were kept until hatched. From 25 to 50 eggs can be cared for in each box in this manner. Upon hatching, each grub was placed in a one-ounce salve box where it was kept until it matured or died. These salve boxes, at times numbering over 5,000, were kept in the rearing cave described by McColloch (1917) in which there was a nearly constant temperature, and thus the grubs were not subjected to the daily fluctuations of temperature in the outdoor insectary. The grubs were examined, with the aid of student assistants, twice a week during the warmer parts of the year, once a week in spring and autumn, and once a month during the winter months, and at each examination the soil was changed and new food (generally a few grains of wheat, which soon germinated) was added, except in the winter when the food was omitted. When a grub reached the prepupal stage, the soil in the box was tightly packed and the grub placed in a depression to simulate a pupal cell. These prepupae were then isolated from the others and examined daily to obtain the dates of pupation and maturity.

All of the species whose life histories are herein discussed were thus handled with the exception of *Pelidnota punctata*, whose habit of living in rotten logs during the larval stage made some changes in the above procedure necessary. This species, the most difficult of any to rear, failed to thrive in individual salve boxes in which rotting pieces of wood were substituted for the grains of wheat. Only one specimen was thus reared. Other specimens, however, were reared in decaying wood placed in one-gallon tins and left undisturbed. This method does not permit the making of observations to determine the molting periods.

One other slight deviation from the general method of rearing was necessary in the case of *Ligyroides relictus* and the *Euphoria* grubs whose larval stage is passed in manure and other decaying vegetable matter. In these cages, instead of feeding wheat grains to the grubs, which, however, they will eat, the soil in which they were placed was made more to their liking by adding to it an equal amount of dried manure.

The material for morphological and taxonomic work was obtained in great part during the course of life-history studies carried on by the writer.

The majority of the specimens were reared from eggs laid by definitely determined beetles. However, certain species which can be distinguished by their habits or the habitat in which they live were studied when their identity was certain. As an example, large grubs found in rotting haystacks can be determined with comparative surety as *Ligyroides relictus* (Say), and other instances could be cited. The molted exuviae of reared grubs were preserved and have proved quite helpful in this study. They possess the advantage of having all the chitinous parts of the mouthparts intact without the presence of muscles and tissues, and this dispenses with necessity of putting them through a clearing process. The molted exuviae are transparent and readily studied and dissected under the microscope.

ACKNOWLEDGMENTS

The collections of the Illinois State Natural History Survey have been used freely through the courtesy of Dr. T. H. Frison, and quite recently the collections of Prof. J. J. Davis, now the property of the U. S. National Museum, have been received for study through the courtesy of Professor Davis, Dr. Adam G. Boving, and Mr. S. A. Rohwer. The latter collections consist mainly of a large number of reared species of Phyllophaga but include also some other genera, three or four of which were not in the writer's collections. Most of the drawings were made by one of my students, Mr. Carl Mohr, through the aid of a grant from the Graduate School of the University of Illinois.

Besides acknowledging indebtedness to the aforementioned persons who have rendered aid in this work, the writer desires to express his gratitude to the officials of the Kansas Agricultural Experiment Station, especially to Professors J. W. McColloch and George A. Dean, under whose direction the life-history studies were carried out.

MORPHOLOGY

The following descriptions of larvae were made in most instances from reared specimens concerning whose identification there is no doubt. A few species were studied which are readily recognizable by their habitus, habitats, or habits, and were not reared because there is reasonable certainty of their correct identification.

The external anatomy of American species of white grubs has been given but slight consideration. Few complete or detailed descriptions of the morphological features are available. With the exception of a few widely scattered descriptions of some known larvae, little has been done. The writer recently (1927) presented somewhat detailed morphological descriptions and figures of the immature stages of *Anomala kansana* H. and McC. Böving's work (1921) on the Japanese beetle has already been mentioned, but nowhere have any comprehensive comparisons been made of American species. Grandi (1925) has presented comparisons of three Italian species. Reference has been previously made to European works on scarabaeid larvae.

The larvae of the Scarabaeoidea (Fig. 1 to 12) are quite similar to one another but easily distinguished from other beetle larvae. The body is elongated, subcylindrical, and in most cases normally bent in the form of a letter C. From this shape is derived the term "scarabaeiform" used to describe this type of larva. The body in many species is nearly constant in diameter from the anterior to the caudal end. In the Cetoniinae (Fig. 11) the caudal end is frequently enlarged, while in many Rutelinae (Fig. 8) it is tapering. The body is distinctly differentiated into a well-formed head and a series of twelve segments making up the thorax and abdomen. The three segments of the thorax bear three pairs of well-formed legs, except in *Passalus* (Fig. 3) which has but two well-developed pairs. The legs are not as important organs in locomotion as they are in digging. In some Cetoniinae the legs are not used at all for walking. Such species crawl upon their back by the aid of body contractions, in which they are assisted by the erect setae with which the body segments are provided. When placed upon their feet, these larvae invariably turn over on their backs in order to move themselves along. The head is more heavily chitinized than the rest of the body, which is paler in color, and the integument is somewhat transparent. The body segments are usually divided into a series of deep folds forming subsegments or annulets. There are usually three subsegments in most of the segments, although in a few species they are indistinct or lacking. The segments in the Lucanidae are less conspicuously subdivided, and in *Passalus* there are no annulets present.

The general body form of some of the coprophagous beetles is distinctly "hump-backed" in outline. This is seen in such genera as *Canthon*, *Copris*, *Pinotus* (Fig. 1), and *Onthophagus* (Fig. 4). Such species usually develop in balls or packs of manure formed by the parents at the time of oviposition.

THE HEAD AND ITS APPENDAGES

The head (Fig. 13 to 24) is hypognathous, that is, situated at right angles to the long axis of the body and with the mouthparts directed ventrad. It is more strongly chitinized than the remainder of the body and varies considerably in color with the various species, ranging from light-yellow or tan in some through all degrees of brown almost to black. The Rutelinae and Melolonthinae contain some of the lighter forms; while the Dynastinae, as represented by *Xyloryctes*, have darker heads. The general form is convex or subglobose (Fig. 13 *et al*) and usually symmetrical, although some species (Fig. 23) are decidedly asymmetrical.

The head capsules of *Phyllophaga crassissima* (Fig. 16), *Ligyris gibbosus* (Fig. 19), *Cotalpa lanigera* (Fig. 20), *Euphoria inda* (Fig. 21), and *Canthon laevis* (Fig. 13) are typical representatives of five separate subfamilies of the Scarabaeidae. In general, they bear a striking resemblance to each other. In color, they vary from a light to a dark tan almost brownish. The size of the head is variable, depending of course upon the instar of the grub and also the species concerned. It has been suggested that the relative size of the head capsule, being thought constant in the various instars, would be of value in distinguishing the different species; but careful observation shows a gradual increase in size between molts.

The cephalic aspect of all species presents the same general gross features, in which is evident the epicranial suture (Fig. 13 *es*) dividing the epicranium, or vertex, and bounding with its branching arms (*ea*) the lateral margins of the front, or frons (*f*). Between the arms of the epicranial suture, on the frons, in *Canthon laevis* (Fig. 13), *Euphoria inda* (Fig. 21), and others, is an extended Y-shaped depression resembling a second epicranial suture and setting off an area quite similar to the adfrontal area found in some lepidopterous larvae. This impression may be a secondary suture. If this condition is an extension of the true suture, it is so closely fused that in *E. inda* there is scarcely any trace of it on the inner surface, while in *C. laevis* the inner surface presents a decided ridge, or carina, which does not extend into the arms. The epicranial suture splits at the time of molting and usually the split is continued into the arms of the Y. In *C. laevis*, however, the split does not extend into the arms, reaching only to the point of branching. In *C. laevis* and in *E. inda* there is a tendency for splitting in the secondary Y. An examination of *E. inda* alone would lead to the conclusion that the secondary Y is merely a depression in the front; but if *C. laevis* is the more primitive of the two, the presence of

the carina may indicate that a suture is disappearing during specialization.

Coincidentally, these two species present a series of four rounded depressions, two on the front and two on the vertex near the arms of the epicranial sutures. At first these suggest remnants of ocelli. In the genera *Trichiotinus* and *Strategus* in which ocelli do occur, they are located near the base of the antennae and seem to have no relation to the depressions in *Canthon* and *Euphoria*. The two depressions on the front are perhaps the external evidence of the points of attachment of the dorsal arms of the tentorium.

The clypeus (Fig. 13 *clp*) adjoining the front is trapezoidal in shape and to it is attached the flap-like labrum (*lab*) with its laterally rounded sides. Laterad of the clypeus and labrum are the prominent mandibles (*md*). The antennae (*ant*) are the only segmented appendages evident on the cephalic aspect, except in *Canthon laevis* where the maxillae may protrude from under the mandibles and thus expose the maxillary palpi. In no case are the labial palpi discernible from this view.

In a caudal view (Fig. 92, 93) with the head removed from the thorax the relatively large occipital foramen (*of*) is seen to be bounded by the fused areas of the postgenae and occiput. Surrounding the foramen is a slight ridge, represented in the drawings by the dotted lines, to which is attached the cervical membrane. The labium is divided into three regions. The submentum (*sm*) is the basal, or proximal, sclerite to which is joined distally the mentum (*m*), and in turn the stipula (*st*) joins the mentum. The maxillae (*mx*) lie laterad of the mentum, and under the maxillae lie the mandibles (*md*).

The heads of the species of the other three families of the super-family—Lucanidae (Fig. 23), Passalidae (Fig. 24), and Trogidae (Fig. 22)—present no striking differences from those of the Scarabaeidae just described. There is a greater tendency for the head to be asymmetrical which is quite pronounced in the head of *Sinodendron* (Fig. 23) and less so in *Trox* (Fig. 22). The head of *Passalus* (Fig. 24) is more like the Scarabaeidae in being nearly symmetrical but is somewhat broader in proportion to its height.

In all species, the head is the most heavily chitinized area of the body. The surface is frequently smooth and impunctate, in other species it is rugose or rugulose. A few setae may be noted. There are frequently four rather conspicuous setae on the clypeus.

ANTENNAE

Three pairs of segmented head appendages are evident from the caudal aspect, the antennae, maxillary palpi and labial palpi. The number of antennal segments has been a matter of discussion. The proximal seg-

ment in nearly all species is fused to the head and not articulate. Some writers disregard it as a segment while others count it as a true division of the appendage. Osten-Sacken (1874) in speaking of the antenna of *Pleocoma* says it is "three-segmented" and does not consider the basal, or fused, region which he termed the "scapus." Schiödte (1874) also disregards it and considers it a "palpiger." Later workers have called it a separate segment, and in this study it will be considered as the first antennal or basal segment. The view of Perris (1877, pp. 93-94) on the number of antennal segments is presented below:

D'après Erichson et les savants naturalistes de Lyon, ces organes seraient composés de trois à cinq articles, le premier n'étant pour eux qu'une saillie tuberculeuse qui simule un article. Je ne puis me ranger à cette opinion. Je ne prétends pas dire qu'elle constitue une appréciation erronée de la structure des antennes, mais comme cette saillie tuberculeuse existe dans toutes les larves, que si, par suite de sa retractilité ou autrement, elle laisse quelquefois place au doute, elle présente habituellement la physionomie d'un véritable article; comme aussi la plupart des auteurs, y compris les entomologistes éminents que je viens de citer, lui ont le plus souvent donné ce caractère dans leurs descriptions, je crois qu'il faut le lui maintenir sous peine d'avoir à rectifier presque tout ce qui a été dit jusqu'ici sur les antennes. Je ferai remarquer en outre que, si cet article basilaire devait être retranché, il serait inexact de dire que les antennes des larves de Lamellicornes ont de trois à cinq articles, car alors il y aurait des larves qui, avec l'article basilaire, en auraient six, ce que je n'ai jamais vu.

In most subfamilies of the Scarabaeidae, the antennae are five-segmented (Fig. 95, 96). The first, or basal, segment being short and conical, the second, third, and fourth are much longer than the first and vary somewhat in size with the different species. The fourth segment at its distal end is frequently extended into a more or less acute or obtuse process (Fig. 95). The fifth segment is usually shorter than the penultimate. In some species it is of fair size and tapers to a point or else ends bluntly. In many of the coprophagous species the last segment is greatly reduced in size and appears almost like a small papilla (Fig. 13) on the end of the fourth segment. Frequently, large sensory pits are evident in the fifth segment. These vary in number in different species in which they occur.

Among some of the coprophagous species of Scarabaeidae, in the Trogidae, and in some Lucanidae, there are but four antennal segments, and in most instances of this sort the terminal segment is small and papilla-like. The antennae of *Passalus cornutus* (Fig. 94) in the Passalidae are but three-segmented. The proximal segment is short but greatly widened, being several times wider than long, or about equal in width to the length of the third segment. The second segment is less widened, somewhat longer, and somewhat conical in shape. The third or distal segment is two or three times longer than wide and somewhat pointed. The composite form of all three segments presents the appearance of a rather uniform cone.

CLYPEUS AND LABRUM

The clypeus presents little that is striking in variation in the different species. It is usually somewhat trapezoidal or subrectangular in outline, and frequently its lateral margins are slightly emarginate, while the proximal and distal margins are usually subparallel. It is much wider than long, and in many species the distal half is less heavily chitinized, with a somewhat sharp line of demarkation, presenting the appearance of a clypeal suture, thus dividing the structure into a preclypeus (Fig. 18, *pc*) and a postclypeus (Fig. 18, *psc*).

In *Canthon laevis* Drury (Fig. 13) the clypeus (*clp*) is about twice as wide as it is long, the anterior and posterior margins are subparallel, and the lateral margins are emarginate and converge slightly distally. The labrum (*lab*) is rounded on the sides, and the anterior margin is distinctive, certain subfamilies having a double emargination that causes the median lobe to appear quite prominent. In none of the forms observed is the labrum exactly symmetrical.

A study of *Canthon ebenus* Say indicates its similarity to *C. laevis*. The clypeus and labrum are quite similar, having as their most conspicuous feature the biëmarginate labrum. *Onthophagus pennsylvanicus* Harold has the same general features of the clypeus and labrum with the biëmarginate anterior margin and prominent median lobe. Perris (1877, pl. 3) figured *Copris lunaris* L. with a labrum of this type, while Osten-Sacken (1862) figured *Pinotus (Copris) carolina* (L.) with an excision in the prominent median lobe. In a study of *P. carolina* specimens before the writer, this excision of the median lobe is not present (Fig. 90, 127). The margin is biëmarginate with a conspicuous median lobe showing no excision as in Osten-Sacken's drawing.

The labrum in the species of *Aphodius* studied—probably *A. fimetarius* (L.)—is biëmarginate, asymmetrical, and trilobed (Fig. 14). It is nearly as long as wide. Schiödte (1874) has figured the labrum of *Aphodius rufipes* (L.) which is quite similar. Both resemble the form of the labrum in *Canthon*.

Phyllophaga crassissima (Blanch.) (Fig. 16) has the clypeus of somewhat the same general shape as *Canthon laevis*. It is trapezoidal in form with the lateral sides less deeply emarginate. The labrum lacks the lobes on the anterior margin and is somewhat pointed. It is as long as broad and circular in outline. The anterior margin is slightly crenate. *Phyllophaga lanceolata* (Say) has much the same general form of clypeus and labrum with no apparent external difference.

An undetermined species of *Diplotaxis* has the clypeus and labrum about twice as broad as the length of either single part. In other words, the combined length of clypeus and labrum is equal to their breadth. The clypeus is trapezoidal in shape, and the labrum is broadly oval. Schiödte

(1874) figures the clypeus and labrum of *Rhizotrogus fallenii* Gyll. and *Serica brunnea* L. with a somewhat different form, especially in the shape of the clypeus. The same is true of his figure of *Melolontha vulgaris* Fab.

The clypeus of *Cotalpa lanigera* (Fig. 20) is nearly three times as broad as long. The anterior and posterior margins are parallel, while the lateral margins are deeply emarginate and converge posteriorly. The labrum is almost as long as broad, subcircular in outline, but not as pointed anteriorly as in Phyllophaga. Both sclerites are larger than in most species. There is a striking resemblance in these sclerites to *Polymoechus brevipes* Lec. except for a proportionately smaller size and the absence of the deep emarginations on the lateral margins of the clypeus.

Anomala binotata Gyll. and *A. kansana* (Fig. 18) have a clypeus without lateral emarginations. It is twice as broad as long. The labrum is slightly broader than long, and the sides converge to a somewhat pointed margin. This point is not as sharp as in Phyllophaga. Schiödt figured *Anomala aenea* De Geer (*Euchlora frischii* Fab.) which also has the clypeus without the lateral emarginations and the labrum of the same shape as in *A. binotata* but with a more deeply rugose surface.

The clypeus and labrum of *Ligyris gibbosus* De Geer (Fig. 19) is proportionately larger than in Phyllophaga, but smaller than *Cotalpa lanigera*, the increase in size over Phyllophaga being expressed in width. The clypeus is trapezoidal, and the labrum is broader and more of an oval than in either *C. lanigera* or *P. crassissima*.

In *Ligyroides relictus* Say both the clypeus and labrum are much broader than long and proportionately larger. The labrum is the most broadly ovate of any of the forms observed. The broad condition of the labrum holds for *Ochrosidia immaculata* (Oliv.) and the anterior margin is noticeably crenate. In comparison with the species of *Ligyris* the labrum is much longer proportionately. There are no important differences in the clypeus.

The clypeus of *Euphoria inda* (Fig. 21) does not converge anteriorly as in the other subfamilies, the whole being nearly a parallelogram with rounded corners. It is twice as broad as long. The labrum has about the same proportions, being broadly ovate with two anterior emarginations producing a small median lobe as in the Coprinae but not so prominent. *Euphoria sepulchralis* has the clypeus of the same rectangular shape and has double anterior margins on the labrum, but is somewhat smaller than *E. inda*. The same characteristics of clypeus and labrum are also found in *Stephanucha pilipennis* K., a rare species of Scarabaeidae that occurs only in Kansas. All of the Cetoniinae noted are more nearly symmetrical than other species studied.

The clypeus of *Trox* sp. (Fig. 22) is unique in being limited proximally by a conspicuously arched fronto-clypeal suture. It is divided into a precly-

peus and postclypeus as in the Scarabaeidae, but with the preclypeus somewhat less heavily chitinized. The labrum is very similar in form to that of the Coprinae.

In the Lucanidae as represented by *Sinodendron rugosum* Mann. the general form of both the clypeus and labrum approaches that of the Cetoniinae in being more nearly symmetrical. No noticeable emargination is present, but the whole is decidedly crenate, and the median lobe is lacking. The clypeus of *Passalus cornutus* Fab. (Fig. 24) is nearly twice as wide as long, and subrectangular. The labrum is subovate with a prominent median lobe on the anterior margin, in this respect resembling that of the Trogidae and the Coprinae.

EPIPHARYNX

The epipharynx, although an internal structure, is one that is easily accessible and can be examined without injury to the specimen by merely inserting a needle under the labrum and raising it up. It can also be studied in living larvae without any apparent harm being done to the individual. The characters of the epipharynx have not been given detailed consideration by previous workers. Schiödt (1874) figured the epipharynx of *Geotrupes*, and his drawing of this genus is copied here (Fig. 58). Böving (1921) has figured and briefly described the epipharynx of *Popillia japonica* Newm. Neither of these writers has attempted to name the various parts. A German worker (Ritterschäus, 1927) has described in some detail the epipharynx of *Anomala aenea* De Geer and *Phyllopertha horticola* L. She is the first to assign names to some of the various parts. Her terms will be mentioned later. The writer (1928) attempted to show the value of the epipharynx as an aid in the discrimination of the various genera. Further study has emphasized the importance of these characters, which are described below in detail because of their use in the generic keys in this work.

The epipharynx (Fig. 25 to 69) is defined as the ental wall of the labrum. Its proximal extent is limited by the tormae, which are situated at the lateral extremes of the clypeo-labral suture. However, a few of the setae and an important sensory area, located between the mesal ends of the tormae, are proximad of this suture and are thus on the ental surface of the clypeus.

The tormae (*t*) are heavily chitinized structures on the ends of the clypeo-labral suture (*clst*) which extend toward the mesal line and in some larvae of this group meet and fuse on the mesal line. In many insects they serve as a landmark in determining the extent of the clypeus and labrum when the clypeo-labral suture is indistinct or absent. In the present group of larvae, the tormae exhibit various sizes and shapes, and further study may find them of more taxonomic importance. They were useful in the separation of *Canthon* and *Onthophagus*. The lateral lobes (*ll*) and median lobes (*ml*), as here considered, apply to the lateral and distal margins

of the labrum of conspicuously biëmarginate species. The lateral striae (*ls*), occurring in Melolonthinae and a few other forms, are short transverse carinae at the bases of setae on the lateral margin. In *Phyllophaga* a second group of carinae, more distal and somewhat removed from the margin, are called submarginal striae (*sms*). On the median line and somewhat removed from the distal margin is an important area, here called the distal sensory area (*dsa*), containing various sensillia and strong chitinous spines. The structures in this region which are, in most cases, obviously strong spines were called by Ritterschaus (1927) "chitinous pegs," and the area upon which they are situated, and upon which are also found numerous pore-like sensillia, was called a "chitinous plate." The chitinous pegs are here called spines (*sp*) and the chitinous plate is the distal sensory area. The sensillia (*sa*) are located at the bases of the spines, being between them and the distal margin.

The proximal sensory area (*psa*) is the region between the ends of the tormae and in many species proximad of the clypeo-labral suture (*clst*). This region contains a strong, rounded tubercle called by Ritterschaus the sense-cone (*sc*). High magnification shows it to contain about four sensillia (Fig. 69). One of these sense-cones is described in detail in the description of the epipharynx of *Phyllophaga futilis*. On the right side of the sense-cone (left in drawings) is a variously shaped, chitinous plate (*cp*), which is not present in some species. On the left side of the sense-cone is a non-setose area which in some forms (*Phyllophaga*) contains 20 to 25 pore-like sensillia. In other species two or three sensillia are found in this area, and in still others none occur. These may be called the clypeal sensillia (*cls*) since they are usually on the clypeus. The remaining surface of the epipharynx is covered with variously arranged articulate setae (*st*), which are usually so arranged as to leave a clear, non-setose area in the center of the epipharynx. Frequently there are interspersed among these setae numerous groups of more delicate, non-articulate spines, especially in the region of the clypeo-labral suture.

Coprinae

Tribe Scarabaeini.—The epipharynx of *Canthon laevis* Drury (Fig. 55) is symmetrical and rather strongly developed and is rather densely covered with strong, hooked setae. The lobe is continued on the ental surface into a prominent, rounded process which bears six shorter setae. There is a central pair of setae arranged transversely, and laterad of these on each side is another pair arranged longitudinally. Still farther laterad are two pit-like structures which somewhat resemble alveoli from which setae have been removed but which are more probably sensoria. The lateral lobes are rather densely covered with long, slender, curved setae. Mesad of these on the ental aspect is located a group of not over a dozen more robust, but shorter, setae which are recumbent, their apices being directed mesad. These are apparently unequal in number on the two sides, with a few more present on

the right than on the left side. Behind, or proximad, of the median lobe in cleared specimens, is a dark, transverse, oval structure which probably would not be apparent in fresh specimens. Near the clypeo-labral suture a few slender setae are grouped on each side; they are recumbent and their points are direct mesoproximad. The tormae are not as well developed as in some other scarabaeid larvae. They appear strongly curved on the sides, and each extends on its mesal end transversely across the epipharynx to meet and fuse with the torma of the other side.

Tribe Coprini.—*Copris tullius* Oliv. (*anaglypticus* Say) also has the labrum symmetrical, strongly trilobed, and biemarginate (Fig. 64). The following description is made from a single specimen whose details are difficult to make out. Its median lobe bears four long setae hooked at the tips and also some shorter setae. The lateral lobes have only a few short setae. No distinct distal sensory area can be distinguished, and there is apparently a group of short setae arranged in the form of a circle. Near the clypeo-labral suture a darker area may be the sense-cone of the proximal sensory area. Other than the circle of setae only a few short, scattered setae are apparent on the ental surface of the lateral lobes. The tormae appear branched, one of the branches being long and extending far onto the clypeus. The epipharynx of *Onthophagus* (Fig. 67) shows quite a different arrangement of the tormae and a somewhat similar circular group of setae in the central area. The distal margin is provided with intermixed long and short, strongly hooked setae.

Aphodinae

Tribe Aphodini.—The species of *Aphodius* (Fig. 56) considered here was taken in large numbers from manure. None having been reared, the specific identity is uncertain, but from the large size of the grubs it is probably *Aphodius fimetarius* (L.), which is one of our largest and most common species. The epipharynx bears comparatively few setae both on the margin and on its inner surface. The margins are smooth proximally but rather irregular distally where they are produced into a broad, single lobe. The widest area is about in the middle, where a single articulate seta is situated with another slightly disto-mesad. Between the broadest point of the lateral margins and the distal lobe six setae, two long and four short, are found on each side. The distal lobe bears two long and four short setae on the margin and about four short setae remote from the margin. Behind the median lobe on each side are two irregularly triangular chitinized areas. Between these and immediately distad of a prominent circle of short chitinous processes, or spines, are two sense-cones. The circle of chitinous processes, or spines, at first glance resembles setae, but they are blunt at their tips, non-articulated, and at the base of some of the distal spines there is an indication of a sensory pore. This circle extends to the clypeo-labral suture.

The tormae meet and fuse on the middle line, whence a chitinous process extends distad to the center of the circle of spines and then expands slightly on the end. On the clypeus are two small chitinous plates found near the fused tormae.

Geotrupinae

Tribe Geotrupini.—No specimens of this genus were available. The drawing of *Geotrupes stercorarius* L. (Fig. 58) is a copy of Schiödte's drawing. In general it is somewhat similar in shape to *Canthon laevis*, being symmetrical and trilobed. The inner aspect has comparatively few setae. The median lobe is strongly produced on the inner aspect. Its margin shows eight strong setae, and eight others, apparently recumbent and directed proximad, are found just within the margin on the inner aspect. A strongly curved, transverse, darker area is proximad of these spines, and two series of small setae, semi-circular in arrangement, are proximad of this darker area. The median lobe is produced into a blunt, rounded process which crosses the clypeo-labral suture. The surface of the lateral lobes bears setae that are shorter and stouter than those of the lateral margins. They are, as in *Canthon*, unequal on the two sides, with a few more present on the right side than on the left. They are recumbent and their apices are directed mostly toward the meson. The tormae are not shown in Schiödte's drawing.

Glaphyrinae

The epipharynx of *Amphicoma* sp. (Fig. 61) is described from specimens in the Davis collection from Hadley, Mass., collected May 29, 1916, by H. E. Smith. Unlike most of the *Laparosticti*, the labrum is only slightly trilobed and only faintly biemarginate. On the margins, both distal and lateral, there are interspersed long and short setae, the long ones being several times longer than the short ones. The median lobe bears the distal area, which is almost on the margin and which contains about twelve sensillia in the form of small, rounded pores. The pores seem to be set off from the rest of the epipharynx by a darker, chitinous, semi-circular band which bears a few setae. The remaining surface of the epipharynx is covered with rather densely placed setae arranged in a circle, with the larger and stronger setae on the distal rim of the circle. In the cleared circle and proximad of the larger setae are a few small rounded areas that may be sensillia or trichopores. The right torma is extremely long, reaching far beyond the median line. The left torma is much shorter. The proximal sensory area, which is behind the right torma in the area formed by a strong curve of the torma, is composed of a strong tubercle-like sense-cone, with two smaller cones to the right. A few minute spines of varying sizes are to be seen proximad of the right torma, and two or three pore-like sensillia are mesad of the sense-cone.

Melolonthinae

Tribe Sericini.—The epipharynx (Fig. 31) is described from specimens in the Illinois Natural History Survey collection, determined as *Serica* sp. by Dr. A. G. Böving. They agree closely with the description of *Triodonta* (*Serica*) *aquila* Cast. by Perris (1877, p. 116). The labrum is more symmetrical than in most of the Melolonthinae and has its distal lobe rather strongly produced. The lateral lobes are margined on the inner aspect by the series of lateral striae. The margins of all three lobes are provided with rather numerous setae, which increase in length distally. There are three prominent spines in the distal sensory area, but no sensillia have been found. Close study may probably show that they are present. The surface of the epipharynx is covered with small setae except for a cleared central space. The tormae are unequal in size and dissimilar in shape. The right torma reaches almost to the median line, and at its end is located the conspicuous sense-cone of the proximal sensory area.

Tribe Melolonthini.—*Diploaxis* sp. is described from a first instar larva (Fig. 34). The epipharynx is broadly oval, with only the distal end bearing setae, about eight in all. The ental surface bears a small patch of comparatively long setae, which are directed meso-distad. They meet on the meson and overlap each other. Between these and the distal margin are a few short, broad setae. The lateral margins lack the series of lateral striae which occur in other Melolonthinae and also in the tribe Anomalini. The distal sensory area is located at the base of four spines with apices directed proximad. Five sensillia can be distinguished at the base of these spines. An irregular series of short setae extends from these spines to the clypeal area. The tormae are poorly developed, the left one being more heavily chitinized than the right, which is almost obsolete. In the area of the epipharynx, distad of the right torma, is a darkened, narrowly chitinized area, which extends disto-proximad. This may be a structure that is not normally present. A small dark area distad of the left torma is probably a sense-cone of the proximal sensory area.

The labrum of *Phyllophaga futilis* (Lec.) (Fig. 37) is asymmetrical, and its distal margin is extended to form a lobe which is covered with a mass of long, slender, articulate setae. The lateral margins are rounded and bear on each side about 16 broad and rather strongly curved, articulate setae. Near the base of each of these setae on the ental aspect is a narrow ridge, or carina, extending toward the meson. This series of carinae give each margin a file-like aspect. They are the lateral striae. Immediately behind the distal lobe and slightly laterad of the meson is another series of ridges, about nine in number. The individual ridges extend nearly disto-caudad, while the series taken as a whole lies obliquely. These are the submarginal striae. Immediately mesad of the submarginal striae on the right (left in sketches) is a darkened, more heavily chitinized area—the distal sensory area. Near

the meson and slightly in front of the middle is a group of six strong spines pointing proximally and having their bases arranged in almost a semi-circle. Three or four other spines of the same nature are situated caudad of the semi-circular group of six. These spines are distinguishable from the neighboring setae by their larger size and the fact that they are not articulate at the base. Distad of the spines and located near their base is a group of pore-like sense-cones arranged somewhat semi-circularly but irregular as to their distance apart. There are six comparatively large cones and five smaller ones alternating with them about the semi-circle. Proximad of the series of spines and sense-cones in the distal sensory area is a large number of articulate, recumbent setae whose apices are directed mesad and meso-caudad. They likewise are semi-circularly arranged, leaving an area in the center with no setae. The series extends to the tormae on the proximal margin of the labrum. On the left of the clear central area (right in sketch), near the proximal margin, is a cluster of long, slender, fixed spines. These lie in part between the branched arms of the left torma. The tormae, located on the clypeo-labral suture, are long, irregular, and asymmetrical. The right torma extends almost to the meson and is unbranched; while the left torma is shorter and is two-branched near its mesal end, with one of the branches, long and slender, extending far onto the labrum. At the mesal end of the left torma is another clump of fixed, slender spines, and mesad of these are about 25 clypeal sensillia. Between these sensillia and the end of the right torma, slightly off the median line, is a triangular chitinized area, almost spine-like, called the chitinous plate by Ritterschaus. It is directed meso-distad. Immediately mesad of the chitinous plate, and apparently partly underlying it, is a broader, less heavily chitinous area pointing in the same direction and covered with long, slender spines (Fig. 69). In cleared specimens, four sense-cones are apparent, which are intermediate between the sensillum ampullaceum and sensillum coeloconium types. Each of these consists of a sunken, fungiform cone which connects with a long, somewhat bottle-shaped canal. The central structure containing the sense-cone is called the "sense-cone" by Ritterschaus. The ental surface of the clypeus, upon which we find the chitinous plate and the area bearing the sense-cones, is called the "epigusta" by some writers (MacGillivray, *et al.*). Just behind the sensory area is a long, transverse, strongly bowed, chitinous bar. All of the structures between the tormae comprise the proximal sensory area.

The epipharynx of *Phyllophaga lanceolata* (Say) (Fig. 26) differs in some detail from the common epipharyngeal form found in this genus, the most conspicuous differences being a more nearly symmetrical outline of the labrum and the presence of only four prominent spines in the distal sensory area. A closely allied species, *P. cribrata* (Fig. 35), is of the typical form, including the usual number of spines on the distal sensory area. Another

species, *P. tristis* (Fig. 27), differs in having but three prominent spines in the distal sensory area.

In the genus *Polyphylla* (Fig. 25), which also belongs to the tribe Melolonthini, the characters are quite similar to those of *Phyllophaga* except for a somewhat different arrangement of the spines on the distal sensory area. The lateral striae are also shorter and less distinct.

Tribe Macroductylini.—The epipharynx of *Macroductylus subspinosus* (Fab.) (Fig. 28) is described from specimens in the Davis collection of the U. S. National Museum. The labrum is asymmetrical, with a single emargination of the distal margin slightly to the right of the median line. The margins, both lateral and distal, are provided with intermixed long and short setae. Lateral striae are present on the inner surface of the lateral margins. Beginning at the notch, or distal emargination, is a more darkly chitinized, irregular plate, which extends proximad to the distal sensory area. In this area is a group of pore-like sensillia arranged in an irregular semicircle. Some of the sensillia are arranged in pairs. From this same area four strong spines are directed toward the clypeo-labral suture. Between the distal sensory area and the clypeo-labral suture a number of setae are arranged in a circle with a non-setose area in the center. The tormae are unequal in size, the left one being considerably smaller than the right. At the end of the left torma is a prominent row of slender, elongate spines. The right torma extends nearly to the median line where the sense-cone of the proximal sensory area is located. In some specimens the cone is a single tooth-like structure, while in others it appears as two teeth (Fig. 28).

Rutelinae

Tribe Anomalini.—The epipharynx of *Popillia japonica* Newm. is quite similar to other species in the tribe. Its close relationship to the Melolonthinae is shown by the presence of the lateral striae, which occur only in these two groups, and by the resemblance in the form and arrangement of the sensory area including the spines, which, however, are fewer in number than in the Melolonthinae. The following species were available for study: *Popillia japonica* (Fig. 41), *Strigoderma arboricola* (Fig. 52), *Anomala orientalis* (Fig. 40), *A. kansana* (Fig. 43), *A. binotata* (Fig. 49), and *A. innuba* (Fig. 46). Except for some variation in the number and arrangement of the spines of the various species, they exhibit rather marked uniformity in structure. The same can be said of *Anomala phyllopertha*, which has recently been described by Ritterschaus (1927). Böving (1921) has figured the epipharynx of *Popillia japonica* but has not given a detailed description of its structure. The labrum (Fig. 41) is strongly asymmetrical, as in the others studied in this tribe except *Anomala orientalis*, which is nearly symmetrical. The distal margin is usually produced into an acute lobe covered with rather long setae. The lateral margins are strongly rounded

and bordered with short, curved setae, at the bases of which are to be found the lateral striae, and with a few extremely long setae intermixed. The distal sensory area has three strong spines and two large articulate setae which might be confused with the fixed spines. At the bases of the fixed spines there are about eight sensillia arranged in a curved line. Between the distal sensory area and the clypeo-labral suture numerous smaller setae are circularly arranged with the customary, smooth, non-setaceous, central area. The tormae are of nearly equal size and do not reach the median line. At the mesal end of the right torma a pointed, chitinous plate and a tubercle-like sense-cone comprise the proximal sensory area. Two pore-like clypeal sensillia are to be found in the cleared area mesad of the sense-cone and proximad of the distal end of the left torma. Latero-proximad of these pores are a number of minute spinules only noticeable under high magnification.

Tribe Rutelini.—Three species of this tribe were studied. They differ strikingly from the tribe Anomalini of the same subfamily and exhibit affinities toward the Dynastinae. *Polymoechus brevipes* Lec. (Fig. 47) is decidedly irregular in outline; *Pelidnota punctata* (L.) (Fig. 44) is more regular and is wider than long; while *Cotalpa lanigera* (L.) (Fig. 50) is longer than wide. The arrangement of the distal sensory area is sometimes hard to make out. It varies more markedly than in the Anomalini. In *Cotalpa* the general form is only slightly asymmetrical, the sides are gradually rounded and no prominent lobes or emarginations are formed. The lateral margins are covered with curved setae which are comparatively short in the proximal region but become longer distally. No lateral striae are present. The distal sensory area is composed of a single chitinous structure produced into a point resembling a spine. Proximad of this structure are a few strong, spine-like, articulated setae. They are directed toward the clypeus, while the remaining setae covering the epipharynx are directed toward the meson with a smooth area in the middle. The tormae are irregular, the left one being curved distad while the right lies transversely. A fold in the integument at the mesal end of the left torma makes this torma appear much longer than it is. At the end of the right torma is the proximal sensory area, composed of a minute, triangular, chitinous plate and a broadly rounded sense-cone.

Dynastinae

Tribe Cyclocephalini.—The epipharynx of *Ochrosidia immaculata* (Oliv.) (Fig. 53) is characterized by the absence of lateral striae along the ental surface of the lateral margins and by the presence of two broad chitinous spines in the distal sensory area. The right spine is nearly twice as broad as the left, and its apex is more rounded. In cleared specimens three sense-cones can be distinguished in this spine. The left spine is more pointed and has at least one sense-cone in it. The lateral margins of the labrum are

comparatively smooth and strongly rounded. They bear about 14 broad and strongly curved setae pointing distally, each of which is slightly longer than the preceding one. The distal margin is more rugose and is armed with a group of long setae. Between this group of setae and the spines described above there is a small, narrow, somewhat curved, chitinous plate, or ridge, which lies obliquely. There are two sense-cones located in the space between this chitinous structure and the two broad spines. A large series of setae of various sizes lie between the spines and the clypeo-labral suture. The setae are inclined in all directions and are so arranged as to leave a cleared area in their center.

The tormae are comparatively short and decidedly asymmetrical. The torma on the left is at first directed proximad, but it soon makes a prominent bend and narrows down toward its extremity, which is near the clypeo-labral suture. The right torma is at first curved proximad but has a less conspicuous curve, so that it extends in an almost transverse direction. At its distal end in the proximal sensory area on the clypeus are two chitinous processes pointing distally. The one almost abutting the end of the torma, and slightly overlapping it, is the larger. This is the chitinous plate. No sensillia were noted in it, but the smaller process which is the sense-cone shows one sensillum. Scattered throughout the large central group of setae are a number of very small dots which are circular in outline and exhibit within them another concentric circle. These are doubtless pore-like sensillia.

Representatives of three other of the five North American tribes of this subfamily have been studied—*Ligyrodes (Ligyru)* *relictus* (Say) (Fig. 42) and *Ligyru gibbosus* DeGeer (Fig. 45) of the Pentodontini, *Strategus antaeus* (Fab.) (Fig. 48) of the Oryctini, and *Dynastes tityrus* (L.) (Fig. 54) of the Dynastini. They differ from *Ochrosidia immaculata* principally in that the chitinous portion of the distal sensory area is produced into a single point, except in *Dynastes* which has two projections located much closer to the margin and much larger proportionally than in *Ochrosidia*.

Cetoniinae

Tribe Gymnetini.—The Cetoniinae are characterized by having the labrum symmetrical and usually biemarginate and trilobed. The distal sensory area is composed of a group of comparatively short, strongly curved setae which are stouter than the remaining setae. In a few species (*Osmoderma et al.*) these setae are apparently not articulate and, as such, are considered as spines.

In *Cotinis nitida* (L.) (Fig. 59) the labrum is deeply biemarginate on its ectal surface but not strongly so on the ental aspect. The trilobed condition of the epipharynx, therefore, is not strongly marked. The lateral lobes have a few short setae, which become more numerous and longer distally. The

median lobe has only a few long setae. It is marked off internally on its lateral areas by a darkly chitinized band extending on each side from the margin to the distal sensory area. Between these bands and at the base of the circular row of setae are two pore-like sensillia. The circular row is composed of about 15 setae, and proximad of these are other setae of similar size. The remaining surface of the epipharynx is covered with longer and more slender setae which become shorter laterally. There is left on the central disk a comparatively small area devoid of setae. The tormae are shorter than in most groups, and the right one is a little longer than the left. Between them in the distal sensory area is a single large sense-cone. The chitinous plate of this area is absent. Some distance proximad of this sense-cone are two pore-like clypeal sensillia.

Among the other species studied in this subfamily, *Trichiotinus piger* (Fab.) (Fig. 66) is the only one that differs radically from others of the group. It was studied in a first instar larva. It does not show the trilobed feature, nor is the circular row of setae in the distal sensory area as marked. *Cremastocheilus* sp. (Fig. 65) was studied from a cast skin in which the epipharynx is nearly devoid of setae, apparently because they were rubbed off, since numerous trichopores are present having the characteristic arrangement of the group. A single sense-cone is present in the proximal sensory area. Three species of *Euphoria* (Fig. 57, 60, 63) are markedly similar, while *Stephanucha pilipennis* Kr. (Fig. 68) appears to lack the sense-cone of the proximal sensory area and has the setae of the distal sensory area more obliquely curved.

Trogidae

This subfamily of Scarabaeidae has recently been raised to family rank. Tillyard (1926) has pointed out in his book, "Insects of Australia and New Zealand," that the Trogidae are intermediate between the Scarabaeidae and Lucanidae. This is also apparent in the larvae in the condition of the stridulating apparatus of the meso- and metathoracic legs and the feebly trilobed anal area, which suggest relationships to the Lucanidae.

The epipharynx of *Trox* sp. (Fig. 39) is symmetrical and neither trilobed nor emarginate. Its lateral margins are almost devoid of setae except distally where five or six large setae are continuous with those of the distal margin. The median distal margin is produced into four conspicuous tubercles, each of which bears a strong seta. The distal sensory area is indistinct, and in the specimens examined its detail is hard to distinguish. Only a few setae are scattered over the lateral lobes, about four on each lobe. The central area is darkened in the specimens, and no detail can be made out. The tormae are small, the right one being the larger. No detail of, or evidence of, a proximal sensory area is apparent.

Lucanidae

The subfamily Dorcinae (Fig. 30), represented in the University of Illinois collection by some larvae labeled *Dorcus* sp. with no other data, lacks the prominent circle of spines found in *Sinodendron* and is more setaceous both on its distal margin and its ental surface. The distal lobes are not so strongly evident, the emarginations being not so marked. The distal margin is densely setaceous, but the lateral margins are nearly bare of setae. The general shape of the labrum is much like *Sinodendron*, being somewhat subquadrate. The entire ental surface is sparsely set with short setae interspersed with small pores which may be sensillia but also may be the trichopores, or alveoli, of setae which have been broken. No circular area of spines is present, but near the middle of one specimen is a semi-circular depression which does not appear to be a normal structure. The tormae are strongly curved at the lateral margin. They extend transversely mesad to unite on the middle line, where another chitinous process projects distad along the mesal line a little more than one-third the distance of the labrum. Behind the fused tormae is a long, narrow sense-cone which is somewhat rounded distally and which ends caudally in three parts. Three, small, cleared areas near its distal end may be sensillia. On the left side of this structure is a much smaller, more transparent, chitinous plate, the distal end of which is rounded. On the right side of the sense-cone is a much larger, backward-pointing, chitinous plate which ends in a sharp point. No trace of sense-cones is evident in these lateral processes.

Aesalinae.—The general shape of the labrum of *Sinodendron rugosum* Mann (Fig. 33) is subquadrate. Its lateral margins are smooth, non-setose, and slightly divergent toward the distal end, where they round off to form the distal margin, which is slightly three-lobed, the lobing being produced by two emarginations, one on each side of the meson. The central lobe bears four setae on its margin and two others that are submarginal. Each of these setae arise from a small papilla. On the ental surface the median lobe is rather strongly convex. On the left of the meson behind the setae is a slight, chitinous spine which is frequently hard to find. Overlapping the median lobe and extending to the clypeo-labral suture is a prominent, almost circular row of spines enclosing a slightly depressed, smooth area. The lateral lobes of the distal margin bear five or six setae, in one specimen five, on the right lobe and six on the left lobe. The rest of the epipharynx is smooth. The tormae are stout on the lateral margins. A pointed process extends meso-distally while another transverse process meets a similar one from the other side to fuse mesally where a pointed projection extends distally along the meson into the clear area surrounded by the circle spines. On the clypeus, proximad of the central chitinized process of the tormae, are two chitinized plates somewhat setaceous on their distal ends, and between these is a long tooth-like process. No sensillia, as found in

Phyllophaga, can be made out in these processes even with the oil-immersion lens. The setaceous distal ends of the lateral plates are probably sensory, while the central process shows under high power a clear central area that may be thinner and may serve in a sensory capacity.

Passalidae

The epipharynx of *Passalus cornutus* Fab. (Fig. 36) is trilobed and nearly symmetrical. The lateral lobes are clothed with a mixture of long and short setae, but the median lobe has only seven setae on its margin and is bare of setae on the ental aspect nearly to the middle of the epipharynx, where there are two rather well defined curved rows of short setae, with their apices directed distally—not as in the epipharynx of other species studied—and laterad of these rows are a number of long setae with their tips directed mesally. No sensillia have been found, but closer study of the distal margin of the median lobe may reveal their presence. The tormae are unequal in size, the left being the larger. They are comparatively small. The present description is made from the specimen shown in Figure 3. Other specimens show the setae of the median area to be arranged somewhat differently.

MANDIBLES

The mandibles (Fig. 70 to 89) are strongly chitinized and somewhat longer than wide. The distal area is usually much darker than the proximal area, which is generally of the same color as the head. A given species may exhibit a marked difference in the shape of the right and left mandible. Perris (1877, p. 93) points out that they are usually provided with teeth, having two teeth on the right mandible and three on the left as a rule. The mandibles exhibit two distinct regions, a proximal and a distal area. Böving (1921) has termed the proximal region the manducatorial region, or the grinding area (also called the molar area, Fig. 81, *mo*), and the distal part the scissorial region (*sc*), or cutting area. The molar area of the left mandible is, as a rule, larger than that of the right mandible. Behind the molar area is a thinly chitinous, setaceous area, the acia (*ac*). This appears to arise on the ventral aspect, where it can be observed that the right acia is long and pointed while the left one is shorter and more rounded. On the dorsal aspect (Fig. 70) is the acetabulum, or preartis (*pa*), by which the mandible articulates with the condyle, or precoila, at the ends of the fronto-clypeal suture. An enlarged sketch of this articulation is shown in Figure 77, in which the preartis is seen to articulate with a condylar precoila (*pcl*). The lateral aspect of each mandible presents a flattened surface, or scrobe (*sb*), bearing a few setae.

The cephalic or anterior surface of the mandibles (Fig. 70 to 80) presents, on the whole, a convex contour, and in all but *Canthon laevis* and a few others it shows two distinct regions limited by a ridge, which is represented

by the dotted lines in the drawings. This ridge, and in most cases a change of contour, indicates the areas covered and uncovered by the labrum when the mandibles are in repose.

The caudal surface of the mandibles (Fig. 81 to 89) presents the notched aspect of the scissorial area (*sc*) in much the same manner as the cephalic aspect but possesses in some species a transversely striated area (*sa*) in the form of an oval. This is part of a so-called stridulating apparatus which occurs in a number of scarabaeid larvae and has been described by Schiödte (1874) and others. Opposed to this series of transverse striations on the maxillae is a variable number of stridulating teeth (Fig. 97, 113, 106 *ms*) which will be described in connection with the maxillae.

On the caudal aspect of the molar area can be noted the acia (*ac*), described above, and in addition, on the right mandible (Fig. 81), a somewhat rounded, lobe-like structure which is apparently absent on the opposite mandible and which overlaps the hypopharynx when the mandible is closed. This lobe plays an important role in the grinding of food. It will be mentioned later in connection with the hypopharynx. This aspect presents a condylar articulation, the postartis (*pta*), on each mandible, which articulates, as seen in Fig. 109, with an acetabular postcoila (*ptc*) located on the gena. Attached to each mandible, but shown in only a few sketches (Fig. 70, 81, 89), are two chitinous processes for the attachment of muscles, which have been described as tendons. The mesal tendon has been termed the rectotendon (*rt*) and the lateral one the extensotendon (*et*). The right mandible of *Canthon laevis* (Fig. 78, 85) has the scissorial area prolonged into a narrow blade with no emarginations forming teeth. The left mandible (Fig. 78, 85) has the regions notched to form three strong and quite distinct teeth, and the manducatorial area has a single tooth larger than the others and truncate at the end. The same area on the right mandible lacks the tooth, but the whole is produced into a convex grinding area that fits into the concave grinding area of the left mandible. This species bears a series of small rugosities in place of the ovate series of transverse, stridulating striae.

The shape of the mandibles in *Canthon ebenus* is not the same as in *C. laevis*. The right mandible has two teeth, and the left has three, on the scissorial area. *Onthophagus pennsylvanicus* seems to resemble *C. laevis* more closely. The right mandible has a long narrow scissorial tooth, while the left has three, and the manducatorial area has one large truncate tooth. The scissorial area of the right mandible of *Phyllophaga crassissima* (Fig. 76, 84) is a long blade-like structure devoid of any notches producing teeth. The manducatorial area is comparatively small, compared to that of the left, and is somewhat concave when viewed on the dorsal aspect. The scissorial area of the left mandible (Fig. 76, 84) is stouter than the right and from the dorsal aspect presents, on the inner side, an irregular margin

scarcely strong enough to be called toothed. When viewed from the ventral side, there appear two rather prominent teeth on the cutting edge. The grinding area is much stouter on the left and bears near its base a strong tooth. *Phyllophaga lanceolata* differs from *P. crassissima* in having a prominent tooth on the scissorial area of the right mandible and two somewhat less conspicuous teeth on the left. The same difference in size of the molar area is here noted as in *P. crassissima*. As in the Coprinae, the transverse, stridulating striae are replaced by a slightly rugose surface.

In *Diplotaxis* the right scissorial area is long and blade-like with a single prominent tooth, and the manducatorial area is small, compared to that of the scissorial region. The scissorial area of the left mandible is proportionately more slender and ends in a sharp point. There are two conspicuous teeth on the inner edge, and the manducatorial region is produced to form a rather noticeable tooth near its cephalic margin. The scissorial and molar areas of *Cotalpa lanigera* (Fig. 74, 83) are proportionately much stouter than in the species of the Melolonthinae studied. The right scissorial area has a serrated inner edge, and the tip end is broadly obtuse. The grinding area is somewhat smaller in the left mandible and bears three conspicuously elevated grinding surfaces. The scissorial region of the left mandible has a small tooth on the cutting edge, which is rather sharp, and the molar surface presents quite an irregular margin, thus differing somewhat from the right mandible.

In *Polymoechus brevipes* the scissorial region is quite similar in both mandibles. The area ends in a rather sharp point, near the tip of which there is a single sharp tooth. The molar areas are of approximately the same size on both mandibles, but one is slightly concave to fit the convexity of the other. The right scissorial area of *Anomala binotata* is comparatively smooth on the inner edge, no teeth being present, and the structure has a rather truncate termination. The left mandible is likewise truncate, but its cutting edge bears two teeth, one rather obtuse and the other acute. The right molar surface is rather flat and smooth and about the same size as the left. In *Anomala aenea*, figured by Schiödt, both the scissorial areas end acutely and the inner cutting edges each bear a single tooth. All Rutelinae studied have an ovate series of transverse stridulating striae. The mandibles of *Ligyris gibbosus* (Fig. 75, 88) are quite dissimilar in shape. The right scissorial area has a smooth cutting edge and is truncate on the end. The left is rounded at the tip, and the cutting edge bears three rather obtuse teeth. The grinding regions are approximately the same size, but the left bears a tooth, as in *Phyllophaga crassissima*, which is lacking on the right molar surface. *Ligyroides relictus* has two obtuse teeth on the cutting edge of the mandible. The right is truncate and the left is broadly rounded as in *L. gibbosus*. Likewise the grinding areas are similar to those of *L. gibbosus*, and the whole mandible is proportionately broader and stouter. The man-

dibles of *Ochrosidia immaculata* are acutely pointed and more slender, and the cutting edge of the left bears two teeth, one of which is obtuse and the other acute, while the grinding surface has numerous teeth with an especially large one at the cephalic margin. The right scissorial area is acutely pointed, and the inner edge has one conspicuous tooth that is obtusely pointed. This subfamily has the transverse stridulating striae on the caudal aspect. The mandibles of *Euphoria inda* (Fig. 73, 82) are proportionately shorter than in the other groups except the Coprinae. The right scissorial region is notched at the end, giving the appearance of a broadly truncated tooth and a small, somewhat acute tooth. The molar area is larger than the cutting region. It is slightly concave and has two teeth. The left scissorial area is truncate at the end and has two large teeth on the cutting edge, while the manducatorial area is convex and bears three broad, short, grinding teeth. All Cetoniinae, as far as known, have an oval stridulating area on the caudal aspect. In the specimens studied of the genus *Trox* (probably *T. unistriatus* Beauv.), the mandibles do not differ strikingly from those of other genera previously described. The stridulating area on the caudal surface is not present. The scissorial area of the right mandible presents a long terminal tooth and another formed by a small notch on the mesal margin. The molar area on this mandible consists of one large, broad tooth and a smaller, but longer, isolated tooth distad of the larger one. The scrobe bears a conspicuous ridge, or carina. The left mandible is quite similar in the scissorial area, and the molar area differs but little in size. Practically the entire structure is very darkly colored. In *Sinodendron rugosum* Mann (Fig. 80) the mandibles are entirely black in color. They are, as in the others, asymmetrical. The distal end of the scissorial area of the left mandible bears three teeth, which are nearly subequal, while the right has but two, of which the terminal one is longer and more slender than the adjacent one. The molar area of the left mandible is larger than that on the right. The stridulating area is absent. In *Ceruchus piceus* (Web.) the dentation of the scissorial area is similar to *Sinodendron*, and the opposing molar areas are dissimilar in shape and size. Specimens of the genus *Dorcus* show no striking differences from *Ceruchus* and *Sinodendron*. In both *Ceruchus* and *Dorcus* no stridulating area is present on the caudal aspect. Perris (1877, pl. 5, fig. 157) shows a right mandible of *Lucanus* with three terminal teeth and no stridulating surface, thus corresponding to the genera here described. The mandibles of *Passalus cornutus* differ considerably from those of the Lucanidae (Fig. 79, 89). The terminal teeth of the scissorial area are three in number on both mandibles, and the molar area is nearly similar on both. It consists of a broad, cup-like tooth, which is strongly depressed on the mesal aspect. Both more nearly approach each other in symmetry than in any other members of the superfamily. The stridulating surface on the caudal aspect is lacking.

MAXILLAE

The maxillae (Fig. 97 to 100 and 103 to 104) present the usual number of parts found in a chewing type except that the galea and lacinia may or may not be fused to form the single structure known as the mala (*m*). The cardo (*cd*) articulates with the postgena (*eg*) (Fig. 109) by an articular acetabulum, the parartis (*pra*), which fits into the paracoila (*prc*) located on the postgena. There are two divisions of the cardo, a subcardo (*sc*) which bears the articulation and an alacardo (*ac*) lying between the subcardo and the stipes. The stipes (*s*) is quadrilateral in outline on the caudal aspect, except at its distal end where it is fused to the mala, while on the cephalic aspect it is not separated from the mala. The palpifer (*pf*) is borne on the dorso-lateral margin of the stipes. On the mesal margin is a narrowly elongate sclerite, the parastipes (*ps*), or subgalea of many authors. A membrane termed the labacoria (*lc*) by MacGillivray (1923) is attached to the inner margin of the cardo, parastipes, and stipes. This membrane attaches to the labium and helps close the oral aperture. The mala (*m*) is densely setaceous and distally bears a series of strong spines (Fig. 115 to 117). In many larvae of the coprophagous Scarabaeidae, all the Lucanidae, Passalidae, and Trogidae, the lacinia and galea are distinctly separate and show no traces of fusion. The series of teeth-like structures found on the cephalic aspect are variable in number (Fig. 111 to 114 and 118, 119, 124, 125), there being usually more on the right than on the left maxilla (Fig. 112). These teeth may point and curve toward the distal extremity of the stipes or may be short, blunt, and not curved (Fig. 113, 118). They usually lie in opposition to the oval, file-like area on the mandible (Fig. 81, 88). These stridulating structures, if such they be, have been described by Schiödt (1874), who asserts that the teeth of the maxillae differ in number and form according to the genera, and further notes that they vary in number from five to twenty, sometimes being straight but more often being extremely sharp and curved. The maxillary palpi (*mp*) are three- or four-segmented.

The cephalic aspect of the maxillae (Fig. 97 to 100, 103, 104) is slightly different from the ventral aspect and will, therefore, be described separately. The cardo is large and subquadrate in all the genera figured. The stipes is limited by a suture from the cardo and may, or may not, be differentiated from the galea, while on the ventral surface there usually appears a suture separating the stipes and galea. The maxillary lobes (galea and lacinia) are separate or bifid in some of the genera, while in others there is a deep longitudinal sulcus which is the limiting line between the two parts.

In the Coprinae (*Canthon laevis*, Fig. 98) the cardo is subquadrate and has a longitudinal suture dividing it into a larger and a smaller area. The stipes likewise is subquadrate and bears on its mesal margin the lacinia which terminates in a single, strong tooth (Fig. 117). On the latero-anterior

margin of the stipes is a smaller sclerite, probably the palpifer or a portion of the galea, from which is articulated the maxillary palpus. Distad of the palpifer is the lobe-like galea which is rounded at the end and bears numerous setae. *Canthon ebenus* also has the two regions, galea and lacinia, separated. The same is true of *Aphodius* (Fig. 100), *Onthophagus pennsylvanicus*, all the Lucanidae, Trogidae, and Passalidae (Fig. 103).

The Melolonthinae, Dynastinae, Rutelinae, and Cetoniinae present much the same appearance dorsally and will not be described separately. In each the cardo is subquadrate; the stipes and galeae are not separated; and the two lobes, galea and lacinia, are fused but are limited on the dorsum by a distinct suture. On the dorsum of the stipes are the stridulating teeth which lie opposite the stridulating areas of the mandibles. Concerning these Schiödt (1874) says:

"Les dents de la tige des mandibules servant à râcler les granulations mandibulaires diffèrent de nombre et de forme selon les genres: il y en a de six jusqu'à vingt et au delà; quelquefois elles sont droites et trèsfortes, mais le plus souvent elles sont extrêmement aiguës et recourbées en crochet."

In *Canthon laevis* (Fig. 119) there are six, large, pointed teeth and a number of very minute teeth immediately cephalad of the larger ones. *Phyllophaga crassissima* (Fig. 118) has fourteen rather blunt or quadrate teeth; *Ligyris gibbosus* (Fig. 124) has thirteen; *Euphoria inda* (Fig. 125) has six, which are long and pointed; while in *Cotalpa lanigera* (Fig. 114) only five rather blunt teeth are found. These teeth have been observed only in the Scarabaeidae.

On the caudal aspect the important differences from those of the cephalic are the sharp delineation of the stipes from the galea, the absence of the longitudinal sulcus marking the fusion of the galea and lacinia, and a few indistinct sutures dividing the cardo into a number of irregular areas. The galea and lacinia of *Canthon laevis* and others with a bifid mala are separate as on the cephalic aspect, while the two are completely fused in other groups. The palpifer is distinctly evident in most species.

The spines and setae found on the galea and lacinia are shown from the mesal aspect in Figures 115, 116, 117, 120, and 121. Upon closer study these may prove of decided taxonomic value. The stronger spines are termed *unci* (singular-*uncus*) by Böving (1921).

Canthon laevis (Fig. 117) has on the terminal end of the lacinia a single uncus. On the fused lobes of *Phyllophaga crassissima* (Fig. 121), there are three rows of unci, with four to six teeth per row. *Ligyris gibbosus* (Fig. 115) has a single terminal uncus and two others standing close together. *Euphoria inda* (Fig. 120) has one terminal and five mesal unci and a number of strong setae.

The fusion of the galea and lacinia seems to be typical of the higher Scarabaeidae. On the dorsal surface of the maxillae there remain traces of

this fusion indicated by the longitudinal sulcus. This condition may be correlated with the food habits. The families Trogidae, Lucanidae, and Passalidae (Fig. 103) all resemble the coprophagous Scarabaeidae in having the galea and lacinia separated.

HYPOPHARYNX

The hypopharynx consists of a densely setaceous area on the ental aspect of the fused glossae and paraglossae and a strongly chitinized area (Fig. 128 to 132), termed by Böving (*loc. cit.*) the hypopharyngeal chitinization (*hc*). The hypopharyngeal chitinization (Fig. 134) is decidedly asymmetrical and somewhat less densely chitinized on the lateral extremities where it is irregularly inflexed to fit snugly against the molar region of the mandibles (Fig. 133) and, in the opinion of the writer, serves as an accessory organ of mastication. The caudal margin of the chitinized area is continuous with the pharynx (Fig. 134), which is probably held open by rod-like structures extending dorsally to the epipharynx. In one preparation it was noticed that there is a direct connection between the ental aspect of the clypeus and the hypopharynx. These connecting bands, of what appear to be slightly chitinized membranes, are shown in Figure 91, extending between the clypeus (*cl*) and the hypopharynx (*hc*). On the dorsal aspect, near the lateral angles, is a series of small setae which are similar to the structures described by Carpenter (1912) as the maxillulae which Crampton asserts are homologous to the crustacean paragnatha.

The hypopharynx consists also of a series of thickly set spines located on the glossa. They vary considerably in the genera studied. Immediately behind the setae is the heavily chitinized, asymmetrical hypopharyngeal chitinization (Fig. 134). The setae of the hypopharynx of *Canthon laevis* (Fig. 130) are arranged in the form of a semicircle and seem in this respect to differ entirely from the other genera studied. In *Phyllophaga crassissima* (Fig. 131) and *Ligyris gibbosus* (Fig. 132) the setae are arranged in a circular group, with their points directed toward the center. In *Cotalpa lanigera* (Fig. 128) they are arranged in a triangle, and most of them are pointed distally. In *Euphoria inda* (Fig. 129) there is a double longitudinal series, one within the other, of setae which tend to converge distally and which point toward the median line.

The hypopharyngeal chitinization of the higher Scarabaeidae is quite similar (Fig. 128 to 134). *Canthon laevis* (Fig. 130) differs markedly. It appears to have the chitinized area divided into two irregular structures both of which are more heavily chitinized on the right side. The structure in the other four genera figured is obliquely transverse and has the right side produced into a more or less blunt end which is more heavily chitinized. The hypopharynx of the families other than the Scarabaeidae has not been carefully studied. In the Passalidae and Trogidae it is more simple, not

being as heavily chitinized, while in the Lucanidae this structure is more pronounced and approaches the higher Scarabaeidae in degree of development. Further study of the hypopharynx may reveal characters of taxonomic value in these structures.

LABIUM

The labium (Fig. 92) is small and usually concealed. It is partly covered on its lateral margins by the maxillae. The submentum (*sm*) is large and somewhat quadrate. It is bordered laterally by the maxillae (*mx*). A smaller, narrow, transverse area represents the mentum (*mt*) which is sharply differentiated from a wider transverse, stipula (*st*). Laterally, the stipula may be prolonged into a deflexed, broadened lobe which is covered by the maxilla. The stipula is broadly rounded on the distal margin. It is strongly setose and bears a pair of small, two-segmented labial palpi (*lp*). Since the labia of the various genera differ from each other less than any other structures of the mouthparts, they are not given extended consideration, although the shape of the various parts differs somewhat, as do also their size and proportion.

THORAX AND ABDOMEN

SEGMENTATION

The thorax (Fig. 1 to 12) consists of the usual three segments, each of which, except in the Passalidae, bears a well-developed pair of jointed legs. The Passalidae have but two pairs of well-developed legs on the pro- and mesothorax and a greatly reduced pair of metathoracic legs. The prothorax (Fig. 8, *I*) may (Fig. 12), or may not (Fig. 1 and 3), be divided dorsally into two or three annulets. The division of the cephalic annulets usually does not extend onto the pleuron. Sometimes a small area of the cervix lying in front of the cephalic annulet is apparent, depending on the degree of extension or retraction of the head. This may cause the prothoracic segment to appear broken up dorsally into four annulets. The cephalo-ventral angle of the propleuron frequently extends forward to partially overlap the head capsule. The propleuron in some forms (Trox, Fig. 7) is more deeply pigmented and slightly more heavily chitinized.

The meso- and metathorax in Passalidae are similar to the prothorax in not being divided into annulets. In all other species noted there are two or three annulets present. In *Pinotus* (Fig. 1) but two annulets occur, while many show three distinct divisions. Perris (1877, p. 94) wrote that the meso- and metathorax, in those species with annulets, were equally divided by a single fold and that the largest division was anterior in the mesothorax and posterior in the metathorax.

The number of abdominal segments is variously counted as nine by some workers (Perris, 1877) and ten by others (Böving, 1921). In *Passalus*

(Fig. 3) there are ten distinctly evident segments, and in many others (*Anomala*, Fig. 8) ten can be easily discerned. Some genera such as *Aphodius* (Fig. 6) and *Euphoria* (Fig. 11) show a tendency towards a coalescence of the ninth and tenth segments. The first eight segments of *Passalus* show a slight diagonal depression tending towards the formation of a small anterior and a large posterior annulet. The *Lucanidae* (Fig. 2) and some of the *Scarabaeidae* (Fig. 1, 4) show but slight annulations. The first six or seven segments of the more common *Scarabaeidae* are thrown into deep folds, forming usually three distinct annulets. The caudal segments are not so constricted. The integument appears stretched and often is partly transparent. The last segment has been called the "sac" by Erichson (1848), which is a term that is used by some European workers to designate the region of the abdomen behind the last spiracle-bearing segment. The sac on its dorsal surface is usually divided by a transversely impressed line which gives in many groups the appearance of two body segments behind the last spiracle-bearing segment. The *Cetoniinae* lack this transverse impression and appear as having but a single segment behind the segment which bears the posterior spiracle.

SETATION

The *Passalidae*, *Lucanidae*, and some *Scarabaeidae*, such as *Pinotus*, are sparsely provided with setae scattered over the body. They are usually lacking in short, stiff spines, except on the ventral part of the last abdominal segment. Most of the *Scarabaeidae* have in addition to the scattered setae a varying number of rows of short, stiff spines that are more noticeable on the dorsal annulets of the anterior body segments and become less dense on the posterior segments. *Amphicoma* (Fig. 139) is especially densely setaceous, and all degrees occur between its condition and that of *Passalus*. The setation of the last ventral segment presents a wide difference in the arrangement of the various spines and setae (Fig. 138 to 191), which have been made use of in the keys in the taxonomic section of this work. These will be described under the term "radula." Arrow (1910, p. 11) points out that the spines on the body aid in progression "and probably also render the grub a less agreeable article of food." It is well known that many *Cetoniinae* do not use their legs but crawl on their backs, and in this they are aided by the dorsal spines.

RADULA

The radula (Fig. 138 to 191) is the rake made up of the spinose and setose area located on the ventral aspect of the last abdominal segment. The function of this structure was described by the writer (1927) as serving as a rake to clean the mouthparts. Ritterschaus in a paper appearing a short

while later (1927) suggests the same function. The radula may or may not possess a median, longitudinal, double row of non-articulating spines, usually recumbent, and with their apices directed toward the median line. Frequent use of the presence or absence of this character is made in taxonomic keys. The setae of the radula are articulate and may or may not be hooked at their tips. This group of setae is frequently figured by workers with white grubs. It has had no name and as far as was previously known no function had been suggested for it. In a study of the digging habits of white grubs in observation cages the writer has frequently noticed the grubs making use of this structure to rake off the mouthparts, which often become covered with soil as the larvae burrow through the soil, especially if it is very wet and sticky. Since the general term "ventral aspect of the last abdominal segment" is cumbersome, it is preferable to speak of it as the rake, or radula. The radula does not differ strikingly in the second or third instars, but in the first instar it is not well developed and some of the spines and setae are wanting.

THORACIC LEGS

The legs (Fig. 101, 102, 135, 136, 137) are normally three pairs, but *Passalus* (Fig. 3, 137) has only two well-developed pairs, with the posterior or metathoracic pair greatly reduced and specialized to function as an organ of stridulation. The nature of this organ and of somewhat similar modifications, but without reduction in size of the metathoracic leg, as occurring in the *Lucanidae*, the *Trogidae*, and some *Scarabaeidae* will be described later when the stridulating organs are discussed.

Following the interpretation of the parts of the leg (Fig. 101, 102) as given by Böving (1921) in his description of the Japanese beetle, we find a long, cylindrical coxa (*cx*) followed by a short trochanter (*tr*). The femur (*fm*) is long and slightly clavate, while the next segment (*tb*) is interpreted as the tibia with the tarsus either absent or, what is more probable, fused with the tibia, since this structure bears the single tarsal claw (*cl*). Arrow (1910, p. 11) considers the claw-bearing segment as the "tibio-tarsus," assuming that the two parts are fused into the one part. It is difficult to say what part is homologous to the small, stridulating leg of the metathorax in the *Passalidae*. In the *Coprinae* no tarsal claw is present.

In most cases, the anterior pair of legs are the shortest, the intermediate pair next in length, and the last pair the longest. The legs are not used to a great degree in walking but are important aids in digging through the soil. As pointed out previously, the *Cetoniinae* do not use their legs in walking but thrust them in the air and crawl on their backs.

SPIRACLES

The spiracles (Fig. 122, 123), although not closely studied, are probably characters of importance for the larger groups. Böving (1921) has described them in some detail for *Popilla japonica* and some allied forms, and Boas (1893) has written concerning the histological features of European Melolonthinae. Schiödte (1874) has also figured the minute structure for some European species. Each spiracle is usually surrounded by a well-defined peritreme (*p*). The peritreme in *Trox* (Fig. 123) is not so well defined and does not resemble that of other species. Normally the peritreme is a half-moon or nearly circular in form. It encloses an area known as the bulla (*b*). The peritreme is usually provided with minute openings or pores. (See the drawings of the two authors cited above.)

The thorax has but one pair of spiracles, located on the caudal margin of the prothorax. There are eight pairs of abdominal spiracles, making nine pairs in all. The meso- and metathorax and the last two abdominal segments are without spiracular openings.

The arrangement of the opening, or emargination, of the peritreme differs considerably in the various groups. In *Passalus* (Fig. 3) the prothoracic spiracle has the open, or emarginate, side of the peritreme on its cephalic margin; while in the succeeding eight segments the emargination is on the caudal margin. In most of the Scarabaeidae (Fig. 8 to 12) the condition found in *Passalus* is reversed; *i.e.*, the emargination of the prothoracic spiracle is on the caudal margin and the remaining spiracles have the peritreme "open" on the anterior margin. In *Pinotus* (Fig. 1) and other Coprinae the emargination of the peritreme of all spiracles is on the ventral margin. In *Trox* (Fig. 123) the shape of the area surrounding the bulla is markedly different from other species. It consists of an indefinite area dorso-ventrally striated and having no definite emargination of the peritreme.

ANAL ORIFICE

The anal opening, frequently called the *anal slit*, is usually figured in published illustrations of the radula. It differs considerably in form in the various groups, and some use of this is made, especially with the Lucanidae, in the appended taxonomic keys. Davis (1916, p. 266), in listing the various characters of scarabaeid larvae, refers to the anal slit as "obtuse" or "transverse." In the obtuse slit a broad angle is formed, with its vertex directed ventrally (Fig. 156 to 189), while the transverse slit is nearly straight or slightly rounded (Fig. 143 to 150). In the Trogidae (Fig. 151) it is Y-shaped, with three slits converging at a central point. This type represents an intermediate condition between that found in the Scarabaeidae and in the Lucanidae. In *Sinodendron* (Fig. 153) and *Dorcus* (Fig. 154), as well as others of the family Lucanidae, the anal slit is made up of three

slits, as in *Trox*. In *Dorcus* and others the slits are surrounded by three more or less conspicuous lobes, which are not so evident in *Sinodendron* and *Trox*. In *Passalus* (Fig. 152) the slit consists of a long transverse opening in the middle of which is a short, ventrally directed slit.

Davis (1916) has pointed out that *Phyllophaga* and *Polyphylla* (Fig. 141) larvae have an obtuse anal slit. The same condition is found in *Serica* (Fig. 140) and *Macroductylus* (Fig. 142) and probably holds good for most of the subfamily *Melolonthinae*. Davis writes: "The grubs of *Anomala*, *Listochelus*, and *Phytalis* are very close to those of *Lachnosterna* [*Phyllophaga*], and we are unable to satisfactorily distinguish between grubs of these four genera." In the case of *Anomala*, they may be separated from *Phyllophaga* by the presence of a transverse instead of an obtuse anal slit. Apparently most of the larvae of the *Scarabaeidae* have a transverse slit, for such is the condition of the specimens examined in the subfamilies *Rutelinae* (Fig. 144), *Dynastinae* (Fig. 145), *Cetoniinae* (Fig. 148 to 150), *Aphodinae* (Fig. 138), and *Glaphyrinae* (Fig. 139).

It is of interest to note that Riley (1870, p. 295) in a description of the larva of *Pelidnota punctata* has figured the anal slit of some lucanid which occurs in decaying wood as does also the larva of *Pelidnota punctata*. He apparently found a newly transformed adult of *Pelidnota* which he associated with the larva of the lucanid that is figured in his article.

ORGANS OF STRIDULATION

The organs of stridulation in lamellicorn larvae are of two types: those of the mouthparts, which are developed on the mandibles and maxillae; and those of the legs, in which the middle and hind legs are modified for stridulation. The stridulating organs of the mouthparts are confined to the *Scarabaeidae* and differ somewhat in some of the subfamilies. The *Lucanidae*, *Trogidae*, and *Passallidae* have no stridulating organs on the mouthparts but have the legs modified to produce sound. Schiödte (1874) was the first to describe these organs, although DeHaan (1836) had previously figured the striae on the mandibles. Schiödte's description of these structures in the *Scarabaeidae* is as follows:

"Chez les larves des *Dynastides*, des *Cétonides*, des *Rutérides*, des *Mélonlonthides*, des *Séricides* et des *Coprides*, il se trouve, sur la face supérieure de la tige maxillaire (*stipes maxillarium*), une crête longitudinale munie d'une rangée de dents disposées de manière à pouvoir atteindre et râcler, par le mouvement d'avant en arrière des maxilles, des granulations spéciales diversement placées et groupées sur la face inférieure des mandibules.

"Les granulations des mandibules chez les larves des *Dynastides* et des *Cétonides* (*Xylotrypes*, *Oryctes*, *Parastasia*, *Cetonia*, *Osmoderma*) sont rangées en côtes transverses assez fortes et formant une plaque à peu près elliptique, nettement circonscrite, située vers la base des mandibules, en dehors de la partie molaire. Les larves des *Rutérides* (*Anomala*, *Phyllopertha*) diffèrent seulement par leurs côtes beaucoup plus fines, plus nombreuses et plus serrées. Chez les *Mélonlonthides* (*Melolontha*, *Rhizotrogus*), des *Séricides* (*Serica*) et des *Coprides* (*Ateuchus*, *Aphodius*, *Ammonoecius*), les granulations des mandibules ne sont pas rangées en

côtes. Chez les larves des deux dernières tribus, elles sont d'une petitesse extrême et placées près de la base des mandibules; chez les larves des Mélolonthides, elles sont plus visibles et occupent un espace transversal au milieu des mandibules."

His article continues with a description of the stridulating apparatus on the legs of Passallidae, Lucanidae, and the genus *Geotrupes* of the Scarabaeidae.

The mouthpart stridulating apparatus, found only in the Scarabaeidae, consists of two types, one being more highly developed than the other. In the larvae of all Rutelinae, Dynastinae, and Cetoniinae examined, there appears on the caudal aspect of each mandible a minute series of sharp ridges, transversely arranged (Fig. 81, 82, 83, 87, 88). The longest ridges are the median ones. The others become gradually shorter to give the whole a uniform oval appearance. Opposite to these ridges of the mandibles, on the cephalic aspect of the stipes of the maxillae, is a row of teeth, which, in some cases, are decidedly blunt (Figs. 118 and 124), in others, long and pointed (Fig. 111), and in still others, long, pointed, and decidedly curved (Fig. 113) toward the distal extremity of the maxilla. They differ in number in different genera. They have not been given careful consideration in this study, but it was noted in *Anomala kansana* that one maxilla bore six curved teeth (Fig. 113) while the opposing maxilla had but one (Fig. 112). One maxilla of *Phyllophaga crassissima* (Fig. 118) had fourteen short, truncate teeth; *Ligyris gibbosus* (Fig. 124) had thirteen; *Cotalpa lanigera* (Fig. 114) five; *Euphoria inda* (Fig. 125) six; and *Amphicomma* sp. (Fig. 111) ten. These teeth, by movements of the mouthparts, rasp against the ridges on the mandibles to produce a "faint high-pitched note" (Arrow, 1910, p. 11).

In the subfamilies Coprinae and Melolonthinae the ridges of the mandibles are lacking, and in their places is a minutely rugose surface which is indefinite and difficult to discern (Fig. 84, 85). According to Arrow (1910, p. 12), this apparatus is comparatively imperfect and it "has not yet been definitely ascertained what sound, if any, is produced by these." The writer has never heard *Phyllophaga* grubs produce any sound.

In the genus *Geotrupes* of the Scarabaeidae, Schiödte and Arrow have both described the leg type of sound production, which is similar to that in the Lucanidae. Arrow points out that the hind leg is considerably shortened and "the joints appear solidified, while from the base to the tip runs a row of sharp horny teeth." These rasp against a horny area at the base of the second pair of legs, which is provided with a series of fine ridges. The rasping structures in this genus, being on the middle leg, are reversed from similar organs in the Lucanidae in which the file, or series of ridges, is on the hind leg. The writer has not seen specimens of *Geotrupes* larvae.

In the Lucanidae (Fig. 135, 136) there is a strongly chitinized area on

the coxae of the middle pair of legs which is covered with small sharp spines or tubercles. On the trochanter of the hind legs is an elongated file composed of a series of transverse ridges. The trochanter of the posterior legs is drawn across the coxae of the middle legs to produce sound. The stridulating organ of *Passalus cornutus* (Fig. 137) is frequently figured in discussions of sound organs because of the unique reduction in the size of the hind pair of legs, the parts of which are reduced to small paw-like structures that are provided with a series of small hooks which are drawn across a microscopically ridged chitinous plate on the coxae of the middle pair of legs. Gravely (1916, p. 139), in a discussion of oriental Passalidae, states that the larvae are all much alike. He figures an oriental species much like our *Passalus cornutus* of North America, which has this modification of the larval leg for stridulation.

Gravely (1915, p. 498) has described the action of the stridulating organs of the mouthparts of *Oryctes rhinoceros* as follows:

"Concerning the action of the stridulating organs of *Oryctes rhinoceros* nothing yet seems to have been published. I have had great difficulty in obtaining any evidence as to the use of the so-called stridulating organ found in the larva. When a specimen is tightly held by the head, however, it may be seen to move the mandibles and maxillae in a manner likely to bring the organ into action, and a faint rasping sound may sometimes be heard if the specimen be brought close to the ear. No definite vibrations have been felt, and the movements of the mandibles and maxillae are those which would probably be used, in order to free itself, by any insect similarly placed. Pressure on the body does not seem to induce any such movements but they are sometimes indulged in by larvae which find themselves on their back on a hard surface in the open. The movements are often greater in extent than their use for stridulating purposes requires; the mandibular part of the organ is, indeed, sometimes fully exposed at intervals, and could not then be scraped at all by the maxillary portion. The rasping seems, nevertheless, to be produced only when these movements occur. It is therefore probable that it is produced by the organs in question, and it is noteworthy that the movement of the mandibles and maxillae is often very small—as it should be to keep the two parts of the organ in contact—and that this does not interfere with the sound produced."

In conclusion of this consideration of these stridulating organs, it must be pointed out that Sharp (1918, p. 198) maintains that these mouthpart structures are "but little adapted for the purpose of producing sound."

POSTEMBRYONIC DEVELOPMENT AND BIOLOGY OF THE SCARABAEIDAE

Since the writer has had no experience with life-history studies of the Lamellicornia other than in the family Scarabaeidae, most of the following statements will be confined to that family. However, it is of interest to recall that the eggs of the Trogidae are laid in carrion while those of the Lucanidae and Passalidae are laid in partly decayed wood. Arrow (1910, p. 20) suggested the possibility of Passalidae being viviparous, but Gravely (1915, p. 495) states that, on a visit to Berlin, he called the suggestion of Arrow to the attention of Dr. Ohaus, who immediately refuted it by producing eggs of American species of Passalidae from his collections.

EGGS

Oviposition Preferences

Among the Scarabaeidae the egg-laying habits are rather diverse, even within the various subfamilies. The eggs of *Canthon laevis* are laid in a ball of dung buried in the soil. *Pinotus carolina* and *Strategus mormon* fill their burrows with manure and afterwards lay their eggs in it. According to Arrow (1910, p. 19), Lefroy has recorded the finding of an egg ball of *Heliocopris dominus* eight feet below the surface of the ground. The progeny of these dung-feeding beetles is not large, some species having been noted to lay less than a dozen eggs; others are more prolific, as Davis (1916, p. 263) has noted that individual females of *Phyllophaga* have been observed to lay between 50 and 100 eggs. In the writer's experience, fewer than 50 eggs was the rule with this genus, but this may be due, in part, to the type of oviposition cages used. The eggs of *Phyllophaga* and other Melolonthinae are laid in the ground, usually in hard, packed soil covered with vegetation, but collection studies show that they are by no means confined to this sort of soil for oviposition, as grubs are frequently found in soil that has been plowed year after year.

Among some Rutelinae (e.g., *Cotalpa lanigera*) and some Cetoniinae (*Osmoderma* spp.) there is an apparent selection of situations for oviposition near decaying wood in which the larvae must develop. The writer has found hundreds of eggs of *Pelidnota* under decaying logs and has succeeded in getting *Osmoderma* to oviposit in soil in cages on which decaying wood had been placed. Other Rutelinae lay their eggs in soil, as do the Melolonthinae, while many Cetoniinae prefer to oviposit in manure and other decaying organic matter. Eggs of the Dynastinae are deposited in decaying organic matter or in the soil about the roots of plants. One species, *Ligyrodus relictus*, lays its eggs in decaying hay and straw stacks, as

well as in manure piles; while a related species, *Ligyris gibbosus*, lays its eggs preferably at the roots of sunflowers. The Aphodinae deposit their eggs in dung, and many species seek out and prefer the excrement of a definite animal.

Description and Length of Egg Stage

The eggs of the Scarabaeidae, being deposited by individuals of many sizes, naturally exhibit enough difference in size to make a general statement of little use. It is obvious that the eggs of smaller beetles, such as *Serica*, some *Diplothesis*, and many others, would be considerably smaller than the eggs of larger species, such as *Dynastes* or *Strategus*. A broad statement might be made, that they vary in size from one to four millimeters. When freshly deposited they are, as a rule, elongate-oval in shape, being two or three times longer than wide. As development proceeds, there is an increase in width, so that the eggs just before hatching are much more broadly oval or nearly round. The color is somewhat variable, even within the species. Some are milky-white, others are pearly-gray. The chorion is transparent, so that previous to hatching the dark mandibles and the segmentation of the body can be discerned through it. With those species which oviposit in the soil, there is usually found adhering to the eggs a sticky secretion from the colleterial glands which causes the surrounding soil to become attached to the eggs and form an enveloping ball of earth around each egg. This ball is usually broken when searching for eggs in the soil, but parts of it can usually be seen still clinging to the egg.

Egg laying occurs in the spring and summer months. It may extend over a considerable period in some species. As far as known, none are ever carried over the winter. Table I, compiled mostly from the writer's observations under conditions as described on page 14, and with the addition of excerpts from other works, shows the length of the egg stage of the Scarabaeidae. It is interesting to note that all of the species listed belong in the four subfamilies of the Pleurosticti, very little being known of the life histories in the Laparosticti.

Egg Burster and Hatching

Many insects possess, in the late embryonic stage, certain spines which aid in the rupture of the chorion during hatching. These have been called hatching spines, ruptor ovi, or egg bursters. In the Colorado potato beetle they consist of three pairs of spines on the thorax, while in other insects the structure may be a single spine on the head. Ritterschaus (1925 and 1927) has mentioned the occurrence of egg bursters in two species of European Scarabaeidae (*Anomala aenea* and *Phyllopertha horticola*). The structure is described as two triangular-shaped, chitinized spines; one on each dorso-lateral aspect of the metathorax. Accompanying the

TABLE I.—THE LENGTH OF THE EGG STAGE IN SCARABAEIDAE

Species	Number of Eggs Hatching	Number of Days			Comment
		Maximum	Minimum	Average	
Melolonthinae					
Strigoderma arboricola...	14	14	10	12.2	
Phyllophaga					
Affabilis.....	54	16	10	14.3	
Bipartita.....	262	24	11	16.6	
Corrosa.....	806	28	11	18.1	
Submucida.....	84	20	13	14.0	Eggs collected in field shortly after deposition.
Vehemens.....	42	28	11	19.8	
Tristis.....	396	23	10	17.2	
Fusca.....	48	28	16	19.5	
Crenulata.....	24	20	14	18.2	
Longitarsa.....	447	19	7	12.7	
Prætermissa.....	185	23	12	17.6	
Ephilida.....	3	15	12	13.0	
Rugosa.....	127	29	14	19.5	
Rubiginosa.....	180	24	11	17.0	
Lanceolata.....	1808	29	10	15.8	
Futilis.....	1017	38	11	21.1	
Crassissima.....	1000	27	8	16.1	
Hirticula var. comosa..	293	30	11	17.9	
Implicita.....	190	31	10	18.2	
Rutelinae—Tribe Anomalini					
Popillia japonica.....	—	27	9	14	Data from Smith and Hadley.
Anomala binotata.....	—	11+	7+	—	
Anomala kansana.....	632	19	9	12.2	
Anomala innuba.....	119	19	11	14.6	
Rutelinae—Tribe Rutelini					
Pelidnota punctata.....	979	26	8	14.9	
Cotalpa lanigera.....	177	27	18	20.9	
Dynastinae					
Ligyryus gibbosus.....	555	22	7	10.9	
Ligyrodes relictus.....	4	11	8	9.3	
Ochrosidia immaculata	107	25	9	15.5	
Strategus titanus.....	—	21	15	17	Data from Smyth.
Strategus quadrioveatus	—	—	—	20	" " "
Dyscinetus trachypygus	—	18	10	12	" " "
Dyscinetus barbatus....	—	—	—	13	" " "
Euethola rugiceps.....	—	—	—	14	Data from Phillips and Fox.
Cetoniinae					
Euphoria inda.....	—	11	7	—	
Euphoria fulgida.....	140	13	8	10.7	
Euphoria sepulchralis...	27	13	9	11.8	
Cotinus nitida.....	8	19	9	13.7	Data from Chittenden and Fink.
Osmoderma eremicola...	—	16	7	16	Data from Sweetman and Hatch.

spine is a stiff bristle, or seta, about twice as long as the hatching spine. Since these are discernible through the chorion before hatching and are not present after the first molt, this author maintains that, by the aid of muscular contractions, they assist the embryo to break the shell during the hatching process.

Such a structure has never been described in North American Scarabaeidae. I have examined many eggs and newly hatched larvae of various species dealt with in this study and have never been able to satisfy myself of the presence of any such a specialized structure. It is true that many strong setae are present, but no strong spine such as described for these European species can be distinguished. Since Ritterschaus has figured these through the chorion of the egg and in larvae which have hatched, it seems probable that further study will show their presence in at least some North American species. It is quite probable that the many strong setae located on the back of most of the body segments aid the insect, in some degree, in its struggle to burst the egg shell.

A scarabaeid egg which is about to hatch can be readily distinguished by its more oval shape in contrast to the elongate-oval form which it presents at the time of oviposition. Moreover, before hatching, the embryo can be seen clearly through the chorion. On the ventral aspect the darkened mandibles are the most distinct, but the tips of the maxillae and antennae can be noted. On the lateral aspect the legs and the darkened spiracles are quite evident, while on the dorsal aspect the body segments and spines can be observed. The mandibles are frequently seen to open and close under the chorion, and perhaps they aid other body contractions in the rupture of the egg shell.

The breaking of the shell occurs across the back in the region of the thorax and first abdominal segments. Ritterschaus (*loc. cit.*) has figured this split as coming directly across the metathorax in the region of the egg burster. The break continues until the dorsum of the thorax is exposed, after which the head is freed and the shell is worked backwards over the end of the abdomen. In rearing cages, many of these newly hatched grubs are unable to remove this shell from the dorsal segments of the abdomen and can be observed carrying it about with them. Sometimes a portion of the shell is cast off over the head. In many instances, newly hatched grubs die before they can entirely free themselves of the egg shell. In a few cases these newly hatched larvae were seen to be feeding on the shell.

LARVAL DEVELOPMENT

Molting

Ecdysis occurs twice before the pupal molt. In two-year grubs as observed, the two molts previous to pupation occur, as a rule, during the same season that the egg is hatched, but rarely the second molt may be

delayed until the following summer. Among the three-year grubs, only the first molt occurs during the season the egg is hatched, and the second occurs the following year. To illustrate: two-year grubs hatching in 1928 would molt twice in 1928 as a general rule, but in a few instances the second molt would be delayed until 1929. The three-year species hatching in 1928 would molt once during the summer of 1928 and once in 1929. All of the grubs molt again at pupation, and generally the pupa lies within the exuvia.

In species having a one-year cycle the customary two molts occur during the growing season of summer and autumn. Occasionally, in *Cotalpa lanigera*, the grubs may undergo three molts before becoming prepupae. The time from hatching to first molt in *Cotalpa* averaged 23.6 days for 49 individuals, and 282.8 days from the first to the second molt, with extremes of 28 and 326 days; that is, some individuals molted the second time during the season in which they hatched and others delayed the second molt until the following season. The period from the second to the third molt varied from 41 to 292 days, with an average of 143.8 days. In no instance was the third molt observed to occur the first season after hatching, but a sum of the three minimum periods shows that it may be possible for the grubs to have their third molt 89 days after hatching. The low minimum of 41 days between the second and third molts was noted in cases where the second molt occurred the second season, and the maximum of 292 days is secured in those instances where the second molt occurred the first season and the third molt the second season.

The period between the second molt and the time of becoming prepupa, therefore, depends upon whether or not there is a third molt. In 19 instances where the third molt was absent, the length of the instar varied from 66 to 432 days, with an average of 334.6 days. In only one case was the time between the third molt and prepupation noted. This individual had molted twice the first season, and the third molt occurred the second summer. There were 379 days between the third molt and prepupa (fourth instar). In all cases (five) where a third molt occurred, the grubs were destined to be three-year grubs. The active larval period varied from 362 to 743 days in 21 cases noted.

The length of each instar, or the period between molts, in the genus *Phyllophaga*, has been taken as the normal period between molts in those individuals having but two molts before pupation. These data are summarized for a few of the representative species in the tables which follow. In Table II is given the average length of time between hatching and the first molt for the species listed. In addition, the maximum and minimum numbers of days between these phenomena are noted, as well as the numbers of individuals under observation. In no case was the minimum period under 11 days (*P. bipartita*), and the longest period occurred in the same species, where 63 days were required before the first molt. The average period ranges from 28 days (*P. affabilis*) to 45 days (*P. vehemens*).

TABLE II—INTERVAL BETWEEN HATCHING AND FIRST MOLT
IN PHYLLOPHAGA

Species	Number of Individuals	Number of Days		
		Maximum	Minimum	Average
<i>P. praetermissa</i>	16	49	19	35.8
<i>P. bipartita</i>	100	63	11	39.9
<i>P. vehemens</i>	2	47	43	45
<i>P. corrosa</i>	237	58	17	39.4
<i>P. hirticula</i>				
var. <i>comosa</i>	41	46	26	35.5
<i>P. crenulata</i>	7	54	35	44
<i>P. affabilis</i>	33	44	23	28
<i>P. tristis</i>	22	52	22	33.9
<i>P. longitarsa</i>	67	42	17	24.1

The length of the second instar is more variable, as is to be noted in Table III, which includes species with a one, two, or three-year life cycle. In general it may be said that the one-year and two-year species listed correspond more closely, in the length of the second instar, to the periods given in the minimum column, while the three-year species and some two-year species more nearly approximate the maximum dates. The shortest period noted for this instar was 7 days (*P. corrosa*) and the longest was 374 days (*P. praetermissa*). This means that the second molt may occur as early as 7 days after the first or as late as 374 days.

TABLE III—INTERVAL BETWEEN FIRST AND SECOND MOLTS
IN PHYLLOPHAGA

Species	Number of Individuals	Number of Days		
		Maximum	Minimum	Average
<i>P. praetermissa</i>	16	374	20	263
<i>P. bipartita</i>	34	335	284	39.9
<i>P. vehemens</i>	2	314	28	171
<i>P. corrosa</i>	136	326	7	218.1
<i>P. hirticula</i>				
var. <i>comosa</i>	41	323	266	294
<i>P. crenulata</i>	1	284	284	284
<i>P. affabilis</i>	19	304	33	198.8
<i>P. tristis</i>	22	28	10	18
<i>P. longitarsa</i>	67	286	11	69.7

To understand the length of the third instar it is necessary, because of the way in which the data were recorded, to present the figures in two tabulations (Tables IV and V). A short time before pupation the larvae cease feeding, shed their meconium, and tend to shrivel up in preparation for the change to the pupal stage. This is the beginning of the prepupal stage. The data on the length of the third instar (up to the prepupal stage) are given in Table IV, and the data on the length of the prepupal stage, which must be added to the figures in Table IV are given in Table V. It will be observed that the third instar is much longer than the others and, as mentioned previously, depends on whether the second molt occurs during the summer in which the larva hatches from the egg or whether the molt is delayed until the following summer.

TABLE IV—INTERVAL BETWEEN SECOND MOLT AND PREPUPA
IN PHYLLOPHAGA

Species	Number of Individuals	Number of Days		
		Maximum	Minimum	Average
<i>P. praetermissa</i>	5	429	320	397.6
<i>P. bipartita</i>	9	423	70	337.2
<i>P. vehemens</i>	2	339	66	202.5
<i>P. corrosa</i>	32	440	97	346.1
<i>P. hirticula</i>				
var. <i>comosa</i>	1	412	412	412
<i>P. crenulata</i>	1	59	59	59
<i>P. affabilis</i>	5	292	35	228
<i>P. tristis</i>	4	372	361	364.7
<i>P. longitarsa</i>	67	388	35	270.6

TABLE V—LENGTH OF PREPUPAL STAGE IN PHYLLOPHAGA

Species	Number of Individuals	Number of Days		
		Maximum	Minimum	Average
<i>P. praetermissa</i>	15	12	3	6.7
<i>P. bipartita</i>	9	17	3	9.2
<i>P. vehemens</i>	3	7	7	7
<i>P. corrosa</i>	25	15	2	6.6
<i>P. hirticula</i>				
var. <i>comosa</i>	25	16	4	8.7
<i>P. crenulata</i>	2	8	7	7.5
<i>P. affabilis</i>	5	5	4	4.2
<i>P. tristis</i>	3	7	5	6
<i>P. longitarsa</i>	58	16	2	4.1

Postembryonic Changes

During larval development there are no conspicuous postembryonic changes. The most marked is the gradual increase in size. This, of course, varies considerably with the different species. Grandi (1925), in a comparison of the newly hatched larva and the larva one-year old, says that there is little difference between them except for dimensions, and goes on further to point out the slight differences which occur in those characters which present variation of any importance. These characters are the antennae, the labrum, maxillae, labial palpi, and abdomen. Of these, he notes that the antennae become longer and more slender; the labrum presents slight changes in shape; in the maxillae the change comes in the proportions of the palpi, and the same is true of the labial palpi and legs. In the abdomen the changes are more marked in the setation of the last abdominal segments. For this reason, the characters in the larval key, as herein presented, are based on third instar larvae, since no satisfactory study has yet been made of the first and second instars.

In addition to the changes pointed out by Grandi, there is a marked change in many species in the proportions of the head and body. In the first instar (Fig. 193) the head is much larger in proportion to the rest of the body than it is in the second (Fig. 194) or third (Fig. 1 to 12). Although no definite measurements have been made, it is quite evident, to one handling and feeding larvae during the summer months, that between the molts there is a slight increase in the size of the head capsule as well as a corresponding increase in the size of the thorax and abdomen. Most of this increase occurs shortly after the completion of ecdysis.

Food Habits

During the course of a series of biological studies of the family Scarabaeidae carried on at the Kansas State Agricultural Experiment Station, considerable data were amassed on the relative numbers, as well as the habitat and food preferences, of larvae of various common species. The results have been published by Hayes and McColloch (1928). Some of the data on the food preferences are taken from that publication and presented here for the sake of completeness.

Collections of larvae of this family of beetles were begun in 1916 and extended over a period of eight years, including 1923. The specimens collected were transported to the laboratory and reared to the adult stage in individual salve boxes in an underground cave. Because of the difficulty in rearing, and in some cases because of the long life-cycle, less than one-third of the numbers collected in the field were reared to adulthood for determination of the species. During the eight years 18,781 grubs were collected, of which 5,884 were matured under artificial conditions. These 5,884 reared specimens represented 17 genera, with a total of

37 species. The largest number of species belonging to a single genus was the 17 species of Phyllophaga. The other genera distributed among the various subfamilies of Scarabaeidae contained but one, two, three, or four species.

In Table VI are shown the habitat preferences of all species collected. These are indicative of the food preferences as a whole but not as related to the individual species, which are shown in Tables VII and VIII. In Table VII it is shown that the most individuals of Phyllophaga were taken in blue grass sod, 234 specimens being found there. The next in preference is corn land, with 140 individuals, which is closely approached by the 126

TABLE VII.—FOOD PREFERENCE OF PHYLLOPHAGA GRUBS

Species	Wheat	Blue Grass and Lawns	Oats	Corn	Logs and Stumps	Pasture	Manure	Orchard	Alfalfa	Potatoes	Garden	Miscellaneous	Total
<i>P. crassissima</i>	23	202	7	45	—	9	2	2	19	5	45	37	396
<i>P. rubiginosa</i>	10	16	1	18	2	16	1	1	16	20	14	20	135
<i>P. rugosa</i>	18	4	6	19	—	3	—	—	6	19	36	14	125
<i>P. lanceolata</i>	45	1	—	5	—	26	1	—	—	—	—	1	79
<i>P. submucida</i>	7	—	2	6	1	3	56	—	—	—	1	3	79
<i>P. implicata</i>	10	1	3	44	1	—	1	1	—	2	4	9	76
<i>P. hirticula</i>	—	—	—	—	—	—	—	—	—	—	—	—	—
var. <i>comosa</i> ...	5	—	9	2	—	1	—	—	6	—	—	1	24
<i>P. praetermissa</i>	2	8	—	—	—	3	—	—	—	—	—	—	13
<i>P. longitarsa</i>	3	—	—	—	5	—	—	—	—	—	—	—	8
<i>P. bipartita</i>	1	—	—	—	1	4	—	—	—	—	—	—	6
<i>P. futilis</i>	—	2	—	—	1	—	—	—	1	—	—	1	5
<i>P. corrossa</i>	1	—	—	—	—	4	—	—	—	—	—	—	5
<i>P. glabricula</i>	—	—	—	—	—	4	—	—	—	—	—	1	5
<i>P. fusca</i>	1	—	1	—	—	—	—	—	1	—	—	—	3
<i>P. crenulata</i>	—	—	—	1	—	—	—	—	—	—	1	—	2
<i>P. tristis</i>	—	—	—	—	—	1	1	—	—	—	—	—	2
<i>P. affabilis</i>	—	—	—	—	—	—	—	—	1	—	—	—	1
Total.....	126	234	29	140	11	74	62	4	50	46	101	87	964

larvae taken from wheat. Pasture land, with 74 grubs, ranks fifth, and probably to this type of food should be added a majority of those listed under the heading "manure" for in many cases these were found on pasture land. It is perceivable that *P. crassissima*, *P. rubiginosa*, *P. implicita*, and *P. rugosa* are quite generally distributed, while *P. lanceolata* shows a preference for wheat first and pasture sod second. The majority of the 56

grubs of *P. submucida* taken under manure were in pasture land. This species seems to have a preference for the upland soils of the region. The data on the other species are limited, but from adult collections it is known that *P. longitarsa* and *P. praetermissa* prefer the sand-hill regions along the rivers while *P. tristis* is usually taken near the oaks growing on the uplands.

The food preferences of other larvae of the family Scarabaeidae are indicated in Table VIII. In the total numbers reared, wheat shows a predominance of individuals, with oats and corn following in the order given. Analyzing the data by species brings out some interesting points. *Ochrosidia immaculata* is taken far more abundantly in wheat than elsewhere, although

TABLE VIII.—FOOD PREFERENCE OF OTHER SCARABAEID LARVAE

Species	Wheat	Blue Grass and Lawns	Oats	Corn	Logs and Stumps	Pasture	Manure	Orchard	Alfalfa	Potatoes	Garden	Miscellaneous	Total
<i>Ochrosidia immaculata</i> ..	1787	32	143	479	49	79	10	3	141	10	138	199	3070
<i>Ligyris gibbosus</i>	125	—	189	17	—	4	11	2	19	—	1	24	392
<i>Anomala binotata</i>	122	2	164	4	—	1	—	—	—	—	—	9	302
<i>Anomala kansana</i>	235	1	2	8	2	1	—	—	1	1	2	3	256
<i>Anomala innuba</i>	5	—	70	—	—	48	—	12	—	—	—	9	144
<i>Anomala undulata</i>	—	8	—	—	—	—	—	—	—	—	—	—	8
<i>Cotalpa lanigera</i>	113	—	—	28	—	—	1	—	6	—	—	1	149
<i>Pelidnota punctata</i>	2	—	—	—	114	—	—	—	—	—	1	1	118
<i>Ligyroides relictus</i>	—	1	—	—	—	2	120	—	—	—	—	—	123
<i>Euphoria inda</i>	—	—	1	—	—	—	41	—	—	—	—	4	46
<i>Euphoria sepulchralis</i> ..	—	—	—	—	—	3	6	—	—	—	—	—	9
<i>Aphodius</i> sp.....	—	—	—	—	—	—	53	—	—	—	—	—	53
<i>Canthon laevis</i>	—	—	—	—	—	4	—	—	—	—	—	—	4
<i>Trox</i> sp.....	—	—	—	—	—	—	—	—	—	—	—	122	122
<i>Polymoechus brevipes</i> ..	—	—	—	—	9	—	2	—	—	—	—	1	12
<i>Cremastocheilus nitens</i> ..	—	—	—	—	21	—	—	—	—	—	—	—	21
<i>Ataenus inops</i>	—	—	—	—	—	—	4	—	—	—	—	77	81
<i>Trichiotinus piger</i>	—	—	—	—	8	—	—	—	—	—	—	—	8
<i>Stephanucha pilipennis</i> ..	—	—	—	—	—	1	—	—	—	—	—	—	1
<i>Polyphylla hammondi</i> ..	—	—	—	—	1	—	—	—	—	—	—	—	1
Total.....	2389	44	569	536	204	143	248	17	167	11	142	450	4920

it occurs rather abundantly in corn and oats. The adults apparently show a preference for land that is frequently plowed. *Ligyris gibbosus* exhibits the same preference, being found most often in oats and wheat and less often in corn land. The same can be said for *Anomala binotata*, while

A. kansana occurs more frequently in wheat. *Cotalpa lanigera* occurs in wheat and corn, usually in the sand-hill area. Davis (1918) has reported this species doing considerable damage to raspberry bushes, strawberries, corn, and grasses.

The following species live in fallen logs and stumps: *Pelidnota punctata*, *Polymoechus brevipes*, *Trichiotinus piger*, and *Polyphylla hammondi*. Table VIII shows 21 individuals of *Cremastocheilus nitens* taken from logs. These were in ant nests on the surface of the soil under a log on the sand dunes. Several species show a preference for manure and decaying vegetation, such as rotten hay or straw stacks. Among these are *Ligyroides relictus*, *Euphoria inda*, *Euphoria sepulchralis*, *Ataenius inops*, and *Aphodius* sp. The 122 individuals of *Trox* sp. listed in the miscellaneous column were taken under a dead horse.

TABLE IX—COLLECTIONS OF PHYLLOPHAGA AS DETERMINED BY REARING

Species	Year of Collection								Total
	1916	1917	1918	1919	1920	1921	1922	1923	
<i>P. crassissima</i>	15	36	40	33	196	52	18	6	396
<i>P. rubiginosa</i>	11	7	15	22	10	41	25	4	135
<i>P. rugosa</i>	14	4	9	33	22	24	14	5	125
<i>P. lanceolata</i>	2	16	9	50	1	—	1	—	79
<i>P. submucida</i>	—	2	2	—	—	—	66	9	79
<i>P. implicita</i>	6	4	4	8	20	1	28	5	76
<i>P. hirticula</i>	—	—	—	—	—	—	—	—	—
var. <i>comosa</i>	—	2	—	—	4	18	—	—	24
<i>P. praetermissa</i>	—	—	3	—	8	—	—	2	13
<i>P. longitarsa</i>	—	1	4	—	—	—	3	—	8
<i>P. bipartita</i>	—	—	1	3	—	—	—	2	6
<i>P. futilis</i>	—	—	—	—	3	—	—	2	5
<i>P. corrosa</i>	—	—	2	—	—	1	—	2	5
<i>P. glabricula</i>	—	2	—	—	—	—	—	3	5
<i>P. fusca</i>	—	—	—	—	—	3	—	—	3
<i>P. crenulata</i>	—	—	1	—	—	—	1	—	2
<i>P. tristis</i>	1	—	—	—	—	—	—	1	2
<i>P. affabilis</i>	—	—	—	—	—	1	—	—	1
Total	49	74	90	149	264	141	156	41	964

Relative Abundance

J. W. McColloch and the writer, in an eight-year study of scarabaeid larvae, made collections of grubs in all kinds of situations and reared many to adulthood. The following discussion of the various collections, for convenience, is divided into two groups. The genus *Phyllophaga*, with 17 species represented, will be considered as one unit while the remaining

16 genera will be considered jointly. Table IX shows the various species as to the year in which they were collected and not the year of maturity. The order of arrangement is based on numbers collected and not on their relationships.

As shown in Table IX, 964 individuals representing 17 species were reared from the total of 18,781 grubs of all species collected. Since many individuals of this genus failed to live through the rearing period, a percentage of those reared based on the number collected would be unfair. However, the percentage reared based on the total species gives an inkling of the relative proportions of Phyllophaga to other species of the family. Of the total (5,884) beetles, only 964, or 16.3 per cent, belonged to this genus. Table IX, as indicated in the column of totals, offers further data on the relative numbers of all the various species found in the locality considered. Of the 964 individuals of all species reared, *P. crassissima* ranks first, with a total of 396 individuals, or about 41 per cent; *P. rubiginosa* ranks second, with about 14 per cent; and *P. rugosa* third, with nearly 13 per cent.

If we compare the individual total of each species with the total adults collected during the first seven years (1916–1922) of the eight during

TABLE X—RELATIVE ABUNDANCE OF PHYLLOPHAGA ADULTS
AND REARED LARVAE

Rank	Species	Total Larvae Reared	Adults Collected 1916–1922	Comparative Ranking of Adult Abundance
1.	<i>P. crassissima</i>	396	31,996	First
2.	<i>P. rubiginosa</i>	135	15,130	Third
3.	<i>P. rugosa</i>	125	4,010	Fifth
4.	<i>P. lanceolata</i>	79	15,851	Second
5.	<i>P. submucida</i>	79	57	Eighteenth
6.	<i>P. implicita</i>	76	982	Tenth
7.	<i>P. hirticula</i> var. <i>comosa</i>	24	1,696	Ninth
8.	<i>P. praetermissa</i>	13	115	Sixteenth
9.	<i>P. longitarsa</i>	8	909	Eleventh
10.	<i>P. bipartita</i>	6	3,523	Seventh
11.	<i>P. futilis</i>	5	10,362	Fourth
12.	<i>P. corrosa</i>	5	3,732	Sixth
13.	<i>P. glabricula</i>	5	440	Twelfth
14.	<i>P. fusca</i>	3	135	Fourteenth
15.	<i>P. crenulata</i>	2	127	Fifteenth
16.	<i>P. tristis</i>	2	114	Seventeenth
17.	<i>P. affabilis</i>	1	44	Nineteenth
18.	<i>P. vehemens</i>	0	2,001	Eighth
19.	<i>P. congrua</i>	0	135	Thirteenth

which this study was in progress (see Table X), some interesting facts are brought out. *P. crassissima*, the most abundant species among the adults collected, is seen to be also the most numerous among those species collected as grubs. *P. lanceolata*, while second in number of adults, is fourth in the grub collections. This may be, in part, due to the slightly longer life-cycle of *P. lanceolata* (Hayes, 1919). *P. rubiginosa*, while third among the adults, was second among the grubs; and *P. rugosa* was fifth in the beetle collections and third among the larvae. On the whole, these four important species rank very close, while greater differences are disclosed among the other species. An interesting observed fact is that more individuals of *P. submucida* were collected as grubs and reared to adults than were taken in the adult collections. The two species, *P. vehemens* and *P. congrua*, which ranked eighth and thirteenth, respectively, in the adult collections, were not reared from grubs.

TABLE XI—THE RELATIVE ABUNDANCE OF SCARABAEID LARVAE
OTHER THAN PHYLLOPHAGA

Miscellaneous Species of Scarabaeid Larvae	Year of Collection								
	1916	1917	1918	1919	1920	1921	1922	1923	Total
Ochrosidia immacu- lata	32	2	155	155	723	315	973	715	3070
Ligyris gibbosus	5	17	2	2	227	23	116	—	392
Anomala binotata	145	4	—	—	37	42	47	27	302
Anomala kansana	—	—	3	1	154	4	57	37	256
Anomala innuba	1	—	9	45	21	—	15	53	144
Anomala undulata	—	—	—	—	—	—	7	1	8
Cotalpa lanigera	—	—	—	—	—	1	23	125	149
Pelidnota punctata	—	2	10	1	1	7	5	92	118
Ligyroides relictus	13	—	10	19	1	74	6	—	123
Euphoria inda	25	—	—	—	1	14	6	—	46
Euphoria sepulchralis	—	—	1	—	—	4	2	2	9
Aphodius sp.	—	—	—	—	—	—	—	53	53
Canthon laevis	—	—	—	—	—	4	—	—	4
Trox sp.	—	—	—	—	—	—	—	122	122
Polymoechus brevipes	—	—	—	—	—	—	12	—	12
Cremastocheilus nitens	—	—	20	—	—	—	1	—	21
Ataenius inops	—	—	—	—	—	—	81	—	81
Trichiotinus piger	—	—	2	—	2	1	—	3	8
Stephanucha pilipennis	—	—	—	—	—	—	1	—	1
Polyphylla hammondi	—	—	—	—	—	—	—	1	1
Total	221	25	212	223	1167	489	1352	1231	4920

In addition to the collections of Phyllophaga, 20 species representing 16 other genera of the family Scarabaeidae are available for comparison with the genus Phyllophaga. These were, for the most part, incidental to the white grub collections, but since all that were found were collected, the data available show the years of abundance as well as the relative numbers. These data are summarized for the various species and the years in which they were collected in Table XI. It will be noted that the two most numerous species are *Ochrosidia* (*Cyclocephala*) *immaculata* (Oliv.) and *Ligyris gibbosus* (DeG.). The number of *Ochrosidia* reared (3,070 individuals) far exceeds that of any other species and is more than three times the number of all Phyllophaga combined, whose total figure is 964. It must be borne in mind, however, that the one-year life-cycle of *Ochrosidia* compared to the two-year and three-year cycles of Phyllophaga makes rearing much easier with less mortality. Space does not permit a discussion of all the facts apparent in Table XI, but it will be noted that the collection contains representatives of the most important subfamilies of the Scarabaeidae.

Hibernation

Our knowledge of the depth to which such insects as white grubs and May beetles penetrate the soil to escape the rigors of cold weather, and to pass their period of hibernation, is limited to a small number of casual observations. Only a few general statements pertaining to the subject are to be found in the literature. While writers assert that such-and-such a species passes the winter "below the frost line" or "below the plow line," no specific attention or careful study has been given to the subject. This is due, in part at least, to the difficulty of studying the habits of insects that live within the soil. Another factor involved, and perhaps the most important, is the difficulty of making specific identification of the immature stages of the specimens found in the soil. In most instances they must be reared through their developmental periods to the adult before they can be identified. Furthermore, winter studies of insects in the soil require careful excavation, involving considerable manual labor which must be done during the coldest and most disagreeable part of the year.

Criddle (1918) records that in Canada the grubs of certain species of Phyllophaga and allied genera penetrate to a depth of 74 inches, and that the beetles may burrow as deep as 47 inches during the winter. This statement indicates at what depth grubs may be found in a more northern climate, but no data are available in regard to the actual depth of the various species in the more temperate regions of the United States. No doubt the climate has a direct bearing on the subject, and the depth of penetration will vary with the region. In fact, the present study shows that white grubs do not penetrate as deeply in Kansas as Criddle observed in Canada. A discussion of the literature of this subject has been presented by McCol-

loch and Hayes (1923), and the following is taken from a discussion by these writers in collaboration with H. R. Bryson. (1928).

The depth at which these insects pass the winter is important in connection with the recommendation of fall, winter, or early-spring plowing as methods of control. In order to make such recommendations intelligently, it is essential to have definite information relative to the depth of hibernation of the insects. It was primarily to secure data along this line that the studies reported herein were undertaken. It also seemed desirable to further check the studies of McColloch and Hayes (*loc. cit.*) in the fall and spring reversals of temperature conditions on the surface and subsurface layers of soil, and the bearing of such changes upon the activities of soil insects in general.

An attempt was made to rear to the adult stage all grubs taken in this work. A summary of these rearings is presented in Table XII, which shows the number of grubs of each species identified and the depths at which they were taken. The data on *Phyllophaga lanceolata*, which are incorporated in this table, were secured from a series of excavations in a wheat field at Goddard, Kansas, March 13, 1919.

TABLE XII—SUMMARY OF THE DEPTH OF HIBERNATION
OF WHITE GRUBS

Species	Total Collected	Depth in Inches		
		Maximum	Minimum	Weighted Average
All white grubs	1,188	40	3	13.2
Ochrosidia immaculata	101	30	4	13.9
Phyllophaga crassissima	3	17	13	15.0
Phyllophaga rugosa	4	26	10	18.0
Phyllophaga glabricula	3	19	16	17.7
Phyllophaga submucida	1	14	14	14.0
Phyllophaga rubiginosa	1	14	14	14.0
Phyllophaga bipartita	1	15	15	15.0
Phyllophaga corrosa	1	16	16	16.0
Phyllophaga lanceolata	66	20	3	10.3
Anomala innuba	99	15	4	8.9
Anomala ludoviciana	2	30	20	25.0
Diploptaxis sp.	1	15	15	15.0
Bolbocerosoma bruneri	5	15	10	11.6

Table XII brings out the fact that the average depth of hibernation of all species was below the plow line. In fact, grubs of only two species were found above the 6-inch level in the work at Manhattan, while a few grubs of *Phyllophaga lanceolata* were taken at three to six inches at Goddard.

While very few determinations were made of the grubs of *Phyllophaga* collected at Manhattan, it is interesting to note that all were several inches below the plow line.

Grubs of *Ochrosidia immaculata* predominated in practically all collections. Out of a total of 101 grubs of this species, only 12 were found above the plow line. The remaining 89 were found at depths ranging from 7 to 30 inches, with the majority at the 14-inch level.

Of *Anomala innuba*, which ranked second in number of grubs identified, 99 specimens were taken. This species does not burrow downward to any great extent for hibernation. The average depth for it was 8.9 inches, with extremes of 4 and 15 inches. *Anomala ludoviciana*, on the other hand, apparently burrows deeply into the soil, as evidenced by the two specimens taken at depths of 20 and 30 inches.

Pupation.—In a previous paragraph mention was made of the preparation made by the larva in anticipation of the transformation to the pupal stage. This period of inactivity, known as the prepupal stage or semi-pupal stage, is of short duration before the actual molt to the pupal condition occurs. The period is characterized by internal activity, a cessation of feeding, some body shrinkage, and the cleaning out of the alimentary canal. The final molt having been completed, the pupa has now assumed a condition more nearly like the adult form. When freshly transformed, the body is a creamy white, but as development proceeds many of the adult colors are assumed. Hayes and McColloch (1920) have pointed out that during the later stages of development sexual differences of the adult may be distinguished in the antennae and the genitalia, which may be discerned through the cuticula of the pupa. In many cases, these characters are apparent throughout the last half of the pupal stage.

Pupation occurs in late summer and autumn in many species (*e.g.*, *Phyllophaga*), and transformation to the adult occurs shortly thereafter, to enable the insect to pass the winter in the adult stage. Others (*e.g.*, *Anomala*) pupate in the late spring and early summer, and at the end of the pupal period, after a few days of inactivity, are ready for flight. In the case of those species transforming in the fall it is usually stated in the literature that the winter is passed by the adult at the place of pupation, usually within the exuvia of the pupa. In observations made by McColloch and the writer there is some reason for believing that many adults leave this place of pupation and burrow beneath the frost line.

No systematic study has been made of the pupae of the Lamellicornia and no keys are available for their identification. Causal observation indicates that there are many differences, and when enough material becomes available it may be possible to describe their recognition characters. It is noteworthy that most pupae of the Melolonthinae are characterized by a pair of pointed caudal appendages, while *Anomala* and a number of other

genera have a rounded, blunt caudal end. Without going into details of the morphology of the pupa, it is sufficient to point out that most of the external characters of the adult are apparent (Fig. 195).

The Passalidae and Lucanidae pass the pupal period in the decaying wood in which they develop. The coprophagous Scarabaeidae, as a rule, pupate and remain within the ball or mass of manure in which the larvae have developed, while higher Scarabaeidae may merely lie within the molted larval exuviae in the soil. A number of Scarabaeidae, such as *Pelidnota punctata* and many Cetoniinae (e.g., *Euphoria*), construct a cocoon in which the pupal period is undergone. In the case of *Pelidnota*, the cocoon consists of fragments of wood, while in the Cetoniinae (e.g., *Euphoria*) it is made of bits of manure in which the larva grew. Others may use the soil or root-fibers. These cocoons, made of the food material, are oval in form. The outer surface is rough while the inner walls are smooth and polished. They are built by the larva before the transformation of the pupal stage, and the material which holds the structure together is a glandular secretion ejected from the hind intestine. The larva, by its mouthparts and body movements, is able to mold the material into a compact water-tight cocoon. The length of the pupal stage in the many species varies from a week or more to a month and even longer in cooler weather. Emergence is accomplished by a splitting of the cuticula along the back.

LENGTH OF LIFE-CYCLE

Melolonthinae

The length of the life-cycle in the subfamily Melolonthinae is extremely variable. It has long been known that *Melolontha melolontha* requires three years for development in France and southern Germany and four years in northern Germany. In Mauritius it has been found that *Phytalus smithi* Ar. has a life-cycle of slightly over one year (De Charmoy, 1912).

Although the species of Phyllophaga have been known as important pests for a number of years, only scanty information has been available concerning their life-histories, particularly with reference to the length of the various stages. This is due, in a large measure, to the fact that practically all of their period of development is spent beneath the surface of the soil, where it is difficult to observe their life activities. Chittenden (1899) was the first to report the rearing of a species of this genus. He found, in the case of one individual of *P. fervida*, that 781 days were required from the date of egg laying to the transformation of the pupa to the adult. This makes a life-cycle of three years for the species if the winter period of adult hibernation is included. Davis (1916), reporting on the length of the life-cycle of 18 species of the genus, notes in his summary that one species, *P. tristis*, invariably has a two-year period in the region of Lafayette, Indiana, and eleven other species, namely, *P. fervida*, *P. fusca*, *P. vehemens*,

P. rugosa, *P. ilicis*, *P. grandis*, *P. fraterna*, *P. hirticula*, *P. inversa*, *P. bipartita*, and *P. congrua*, without exception, have a three-year life-cycle. Two species, *P. crenulata* and *P. crassissima*, have a three-year cycle that may be extended to four years, and certain other species, as *P. futilis*, *P. ephilida*, and *P. implicata*, ordinarily have a three-year cycle that is often reduced to two years. From this it can be seen that the more important species have, in the latitude of Lafayette, a three-year cycle. Smyth (1917) has found that the life-cycle of *P. vandinei* occupied approximately one year in Porto Rico. These citations contain practically all our knowledge of the life-cycle of members of the genus, and except for the work of Smyth very little has been learned concerning the length of the immature stages.

In a study of the life-history and development of white grubs carried on by the writer in Kansas, seventeen species of the genus *Phyllophaga* were reared in varying numbers from the egg to the adult state. The development of one species, *P. lanceolata*, was described in 1919 and six others in 1920. In 1925, ten others were described and a comparison of their development made with those previously reported. To generalize, it can be asserted that the results are in accord with those of Davis in showing a decided variation of the length of the life-cycle in most of the species, this variation being found in the length of the larval period. For example, some species have, in the vicinity of Manhattan, Kansas, either a one-, two-, or three-year life-history.

With the exception of four species, *P. affabilis*, *P. submucida*, *P. longitarsa*, and *P. lanceolata*, all of the *Phyllophaga* reared by the writer pupate in the fall and pass the winter as adults. Accordingly, in considering the life-cycle, eight or nine months should be added to the figures presented in the following table to arrive at the total period of life from the time of oviposition to the normal time of death. In the four exceptions noted above, pupation occurs in the spring or early summer and the adults emerge soon after transformation.

To further compare the life-cycle of *Phyllophaga*, it should be noted that Davis (1916) found a two-year cycle in *P. tristis* and *P. lanceolata*; a two- and three-year period for *P. burmeisteri*, *P. futilis*, and *P. implicata*; a three-year period for *P. arcuata*, *P. bipartita*, *P. congrua*, *P. fraterna*, *P. fusca*, *P. grandis*, *P. hirticula*, *P. ilicis*, *P. inversa*, *P. rugosa*, and *P. vehemens*; and a three-year and possibly a four-year cycle in *P. crassissima* and *P. crenulata*.

Smyth (1917), in Porto Rico, found for 14 complete records of *P. vandinei* an average period of 306 days from egg to adult with a maximum of 395 days and a minimum of 212 days, or expressed in months, from seven to thirteen months with an average of about ten months. Except in the case of *P. tristis*, this is one of the shortest life-cycles reported. It is somewhat shorter, but is probably comparable to the one-year periods of

P. affabilis and *P. longitarsa* as here recorded. Criddle (1918) reports that *P. nitida*, *P. drakii*, *P. anxia*, and *P. rugosa* have in Manitoba, Canada, a four-year life-cycle, but gives no definite data on the length of the various stages.

Based on actual rearings by the writer, the summaries of the life-cycles of the 17 species under observation are given in Table XIII.

TABLE XIII—SUMMARY OF THE LIFE-CYCLE IN THE GENUS PHYLLOPHAGA

Species	Number of Individuals Reared	Number of Days from Egg to Adult			Life-cycle in Years
		Maximum	Minimum	Average	
<i>P. affabilis</i>	4	389	369	376.6	1
<i>P. bipartita</i>	3	815	495	703.0	2 and 3
<i>P. corrosa</i>	19	791	429	501.8	2 and 3
<i>P. submucida</i>	13	734	708	720.3	2
<i>P. vehemens</i>	3	838	459	591.3	2 and 3
<i>P. tristis</i>	4	474	137	380.0	1 and 2
<i>P. fusca</i>	1	461	461	461.0	2
<i>P. crenulata</i>	1	424	424	424.0	2
<i>P. longitarsa</i>	48	701	327	356.4	2 and 3
<i>P. praetermissa</i>	2	811	434	628.5	2 and 3
<i>P. rugosa</i>	21	836	445	735.7	2 and 3
<i>P. rubiginosa</i>	29	839	447	791.5	2 and 3
<i>P. lanceolata</i>	23	723	357	675.7	1 and 2
<i>P. futilis</i>	16	494	457	469.7	2
<i>P. crassissima</i>	81	816	449	588.3	2 and 3
<i>P. hirticula</i> var. <i>comosa</i> ...	2	789	780	784.5	3
<i>P. implicata</i>	22	790	442	470.4	2 and 3

Other members of the subfamily are little known. The rose chafer, *Macrodactylus subspinosus*, has been studied and found to have a one-year life-history. Other important genera, such as *Polyphylla*, *Serica*, *Diplo-taxis*, and *Dichelonyx*, are practically unknown as far as knowledge of their life-history is concerned.

Rutelinae

It is evident that there are two distinct types of development in the two tribes of the subfamily Rutelinae. In the tribe Anomalini there appears to be invariably a one-year life-cycle, while in the tribe Rutelini it is known that at least two years and often three years are needed to complete the life-history.

In the Anomalini, Hadley (1922) has pointed out that *Popillia japonica* requires one year to develop. The writer (1918) has shown that *Anomala binotata* matures in one season. The larvae require, on an average, 83

days to develop, and pupation occurs in the fall. On the contrary, *Anomala innuba* normally matures in the spring, but only requires one year to complete growth. Two instances were noted wherein the larvae of *A. innuba* pupated in December. *Anomala kansana* also has a life-cycle quite similar to that of *A. innuba*. It has also been shown (Hayes, 1921) that *Strigoderma arboricola* Fab., another Anomalini, has a one-year life-cycle, in which development is completed in from 351 to 358 days. In this case the larvae pass the winter and pupate in the spring. In the tribe Rutelini, *Pelidnota punctata* requires two years to mature, while *Cotalpa lanigera* needs either two or three years (Hayes, 1925). A summary of the life-cycle in this subfamily, based mostly on rearings by the writer, is given in Table XIV.

TABLE XIV—SUMMARY OF THE LIFE-CYCLE IN RUTELINAE

Species	Number of Individuals Reared	Number of Days from Egg of Adult			Life-cycle in Years
		Maximum	Minimum	Average	
Anomalini					
<i>Anomala binotata</i>	—	100	119	—	1 year
<i>Anomala innuba</i>	—	330	356	342.9	1 year
<i>Anomala kansana</i>	16	376	339	368.3	1 year
<i>Strigoderma arboricola</i>	4	351	358	—	1 year
<i>Popillia japonica</i> ^a	—	—	—	—	1 year
Rutelini					
<i>Pelidnota punctata</i>	1	698	698	698	2 and prob- ably 3 years
<i>Cotalpa lanigera</i>	21	416	806	604.6	2 and 3 years

^a Data on maximum and minimum periods not available.

Dynastinae

The subfamily Dynastinae is remarkable for the fact that it contains some of the largest coleopterous insects. One has only to recall such genera as *Dynastes* and *Strategus* to realize this fact. The group contains a number of species whose depredations on crops make them of considerable economic importance, especially in the southern part of the United States and in the West Indies. One species, *Ochrosidia (Cyclocephala) immaculata* Burm., is very injurious in the larval stage to the roots of staple crops in the central states; and another, *Ligyris gibbosus* DeGeer, known as the carrot-beetle or muck-worm, is destructive in the adult stage to carrots, sunflowers, and other plants. Both of these have been under observation during the course of this study. *Ochrosidia immaculata* has been reported under the name of *Cyclocephala villosa* (Hayes, 1918) and the life-cycle was given as one year. Likewise, *Ligyris gibbosus* was found (Hayes, 1917)

to have a one-year life-cycle. *Ochrosidia* differs from *Ligyris* in passing the winter as a larva and maturing in the spring.

Smyth (1916) has reported on the period of development of five species representing three genera of this subfamily. He found that *Strategus titanus* Fab., in Porto Rico, required an average of 338 days to reach maturity, *Strategus quadrioveatus* Beauv. required slightly over one year, and *Ligyris tumulosus* only 77 days. Two other species, *Dyscinetus trachypygus* and *Dyscinetus barbatus*, complete their growth in 104 and 144 days, respectively. Phillips and Fox (1917) report the development of *Euetheola rugiceps* in about 88 days. Smyth (1920) made further reports on the life-cycle in *Strategus*.

The writer has reared three species of this subfamily, *Ligyrodes relictus*, *Ligyris gibbosus*, and *Ochrosidia immaculata*. A summary of the chief points of interest in their development is given here.

Adults of *L. gibbosus* are present in the soil throughout the winter and early spring. During the latter part of April or the first few days of May, and continuing throughout the summer, they emerge at night and fly to lights, returning to the soil before daybreak. During the summer of 1916, eggs were plentiful from the last of May to late in July. Larvae were present from June throughout the remainder of the summer and early fall, and pupae from the last of July to the last of October. The length of each stage of development is shown in Table XV.

Ligyrodes relictus is to be regarded as a beneficial species, living as it does in manure and rotting haystacks and thus materially hastening the processes of decomposition. Smith (1902) reported the beetles injuring the roots of hardy pyrethrums and the roots of sunflowers, but his statement that the species is smaller than the ordinary June-bug and more roughly sculptured, leads to the suspicion that his determination was incorrect. These two characters and the habit of attacking sunflowers would suggest that *Ligyris gibbosus* was the species in question. Smith appears to be the only writer who considers *Ligyrodes relictus* as an injurious species. There are no citations in the literature treating of the life-history of the species, and scarcely any habits are mentioned except that the beetles and grubs live in decaying vegetable matter. The average periods of development of the different stages have been found to be: for the egg stage, 9.3 days; the active larval period, 46 days; the prepupal period, 4.1 days; and the pupal period, 13.1 days. The total of 72.4 days for complete development thus approximates very closely the full period computed from the length of the different stages. Davis (1916) has reported that the species develops in one year, but gives no data on the length of stages. The beetles appear above ground in April or May for the spring flight, returning to the soil each day, where mating occurs. They disappear for a short time in June

and July, and the new brood appears in July and August for a second period of flight.

The genus *Ochrosidia* (*Cyclocephala*) contains some of our common and most injurious white grubs. Forbes (1891, p. 40) reports the grubs of *O. immaculata* infesting grass-land, corn on sod, roots of corn, and young oats. Titus (1905, p. 14) found them at the roots of grass and sugar-cane stubble, and Riley (1870, p. 307) recorded them in strawberry beds. Davis (1916, p. 264) states: "*Cyclocephala immaculata* is frequently found in compost heaps and in cultivated fields, and may obtain its full growth on decaying matter alone or may become a serious field pest, damaging crops similar to those attacked by *Lachnosterna* grubs." To summarize, the life-cycle of *O. immaculata* is one year. Adults appear at lights in June, July, and early August. Eggs, which are laid in soil, hatch after 9 to 25 days. The larva passes the winter in hibernation. The larval stage was found to average 347 days. The pupal stage varied in length from 8 to 24 days.

A comparison of the life-cycles of these three species with others reported in the literature is given in Table XV. In this table it is to be noted that, of the species whose life-history is known, the average period of development ranges from 72 days, or slightly over two months for *Ligyrodes*, to 430 days, or more than a year, for *Strategus quadriveatus*.

TABLE XV—SUMMARY OF THE LIFE-CYCLE IN DYNASTINAE

Species	Egg Stage			Larval Stage			Pupal Stage			Egg to Adult
	Average	Max.	Min.	Average	Max.	Min.	Average	Max.	Min.	Average
<i>Ligyrodes relictus</i>	9	11	8	50	—	—	13	26	9	72
<i>Ligyris tumulosus</i> ^a	13	—	—	55	—	—	14	—	—	77
<i>Ligyris gibbosus</i>	10	22	7	59	80	43	19	29	11	88
<i>Ochrosidia immaculata</i>	15	25	13	347	384	335	17	21	15	379
<i>Strategus titanus</i> ^a	17	21	15	344	—	—	23	24	—	338
<i>Strategus quadriveatus</i> ^a	20	—	—	385	—	—	27	—	—	430
<i>Dyscinetus trachypygus</i> ^a	12	18	10	81	—	—	13	16	12	104
<i>Dyscinetus barbatus</i> ^a	13	—	—	106	—	—	15	18	13	144
<i>Euetheola rugiceps</i> ^b	14	—	—	60	—	—	14	—	—	88

^a Data from Smyth (1916).

^b Data from Phillips and Fox (1917).

Arrow (1910, p. 259), in his summary of the habits and metamorphoses of this subfamily, points out the following facts. They are mostly confined to the warmer climates and are of somewhat retiring habits, and our knowledge of their metamorphoses and modes of life is exceedingly scanty. With but few exceptions they are nocturnal or crepuscular and are not easily

found, and in few cases have their early stages been traced. He points out the increase in the size of the eggs, which is discussed on a previous page, as being characteristic of most scarabaeid eggs. Further comment is made that the larvae "do not differ in any marked degrees from those of the Cetoniinae and allied subfamilies," and like the Cetoniinae feed upon decaying vegetable matter, and sometimes upon living roots or woody tissues. A discussion of the nest-building habits of *Strategus antaeus*, as quoted from Manee (1908), shows these larvae to feed first on leaves stored in the nest and then probably on oak roots. Various Dynastinae are known to feed on the roots of grasses, one is known to destroy the roots of sugar cane, and *Oryctes nasicornis* is found in the refuse-heaps of tanneries, where the larvae feed on the decomposed bark.

Cetoniinae

Several members of the subfamily Cetoniinae are injurious to vegetation in the United States. Chief among these are the bumble flower-beetle, *Euphoria inda*, and the green June-beetle, or fig-eater, *Cotinus nitida*. As a rule, the mandibles of the adults of this subfamily are poorly developed and are fitted only for the eating of such light foods as pollen and sap.

There is very little American literature on the life-history of American species of this group. *Euphoria inda* is commonly assumed, and probably correctly, to have a one-year life-cycle, and the green June-beetle, *Cotinus nitida*, has been reported by Chittenden and Fink (1922) to have a one-year period of development. In the present study, a number of species have been under observation, such as *Euphoria inda*, *Trichiotinus piger*, *Osmoderma eremicola*, and *Cremastochelius nitens*. The life-cycle of none of these has been completely worked out, but two species, *Euphoria fulgida* and *Euphoria sepulchralis*, have been carried through to maturity and the results are here summarized (Hayes, 1925).

TABLE XVI—SUMMARY OF THE LIFE-CYCLE IN CETONIINAE

Species	Number of Days from Egg to Adult			Length of Life-cycle
	Maximum	Minimum	Average	
<i>Euphoria fulgida</i>	434	323	381.3	1 year
<i>Euphoria sepulchralis</i>	123	74	92.9	1 year
<i>Euphoria inda</i>	—	—	—	1 year
<i>Cotinus nitida</i> ^a	—	—	—	1 year
<i>Osmoderma eremicola</i> ^b	—	—	—	3 years

^a Data from Davis and Luginbill, 1921.

^b Data from Sweetman and Hatch, 1927.

Arrow (1910, p. 24) says of this subfamily, "Of the metamorphosis and habits of the species we know lamentably little." There are, according to him, about 2,500 species in the world. Of those occurring in America but few are of economic significance, and except for the green June-beetle, *Colinis nitida*, three species of the genus *Euphoria*, and one of *Osmoderma*, nothing has been done toward working out their life-histories. Recently Sweetman and Hatch (1927), in rearing a larva of *Osmoderma eremicola* for 18 months, concluded that, allowing for outdoor periods of hibernation, the life-cycle would be three years for this species. It is interesting to note that all whose life-cycle has been studied require but one year to develop while *Osmoderma* with entirely different habits requires a much longer time. The little that is known of the development in this subfamily is summarized in Table XVI.

Laparosticti

For an interesting account of the biology of the Coprinae and other dung-feeding larvae, the reader is referred to Fabre's *The Sacred Beetle and Others* (English translation, 1924). Here is to be found this author's study of the development of the sacred beetle (*Scarabaeus sacer*), the *Gymnopleuri*, *Copris*, *Onthophagus*, and *Geotrupes*. Space will not be taken here to quote it. No complete American work has been done on any of our species of the subfamily. Neither has there been any investigation into the length of life of our Aphodinae. The following account of this subfamily is a translation of Schmidt's account in *Genera Insectorum*, fascicle 110, (1910).

The life-history and development of the Aphodinae are little or not well known. It is generally observed that their eggs are laid in dung, from which the developing larvae obtain their nourishment, and that pupation occurs in or under the food material. Many species apparently prefer and seek out the excrement of a definite animal. Certain species develop in the excrement of the sheep or deer, others in that from cattle, some from horses; while others may prefer either that of horses or cattle. Certain European species are known to develop in human wastes. Hubbard has reported *A. troglodytes* as living in the burrows of the land tortoise, *Gopherus polyphemus*, and Chapman states that *A. porcus* lays its eggs in the brood chambers of the scarabaeid larvae, *Geotrupes*, or the material upon which the *Geotrupes* feed. Another species occurs only in rabbit dung. *Psammobius* and *Rhyssemus* inhabit sandy regions. Their habits have not been studied, but it is thought that some species of *Rhyssemus* live on vegetable materials while others live in dung. Ohaus has noted some species of *Ataenius* in dung and others under the bark in rotten wood of fallen trees. Some exotic genera of this subfamily (*Euparia* and *Friedenreichi*) live with ants, while others (*Chaetopisthes*, *Corythoderus*, and *Termitodius*) inhabit termite dwellings.

TAXONOMY

Early students of American insects confined themselves to a study of the anatomy and classification of adult insects and the working out of their life-histories. This has resulted in descriptions of numerous new genera and species from adult characters and the description of the eggs, larval and pupal stages, and the host plants of numerous species. The number of known life-histories has been greatly increased by the establishment of state and federal experiment stations and the appointment of entomologists for the study of injurious and related species. There has been a great increase in the number of persons interested in the study of immature insects; and there have been published, not only in Europe but also in America, many systematic studies attempting to furnish tables for the identification of immature as well as adult insects. All classification is based on anatomical characters and any attempt at identification must be preceded by morphological studies. The anatomy of immature insects in many cases, while similar in general to that of the adults, is frequently very different, especially when the insects are examined in detail. The larvae contain many structures peculiar to themselves, being in most cases fitted to live a life very different from that of the adults.

A study of the anatomy of immature insects is of value from three points of view: ontogeny, morphology, and classification. It has been shown repeatedly that the complete history of the individual—its ontogeny—throws much light upon the relationship of organisms and upon their differentiation, not only as to species and genera but also as to families and orders. Investigators have found that what had been considered as a single species, from a study of the adult alone, proved to be a complex of two or more species when the immature stages were known, and that characters previously believed to be worthless could be used for separating the adults. Ontogenetic and morphological studies should proceed hand in hand. Many structures that are complex and difficult to interpret in the adult are easily understood by a comparison with the conditions found in immature insects. By comparative studies of this sort, the homology and homodynamy of various structural parts are easily determined. While it is impossible, without at least some morphological knowledge, to attempt the identification of adult specimens, such knowledge is equally pertinent for one undertaking the study of the anatomy of immature insects. The classification and identification of such insects is of the greatest value to the economic

worker, because the investigator in this field almost invariably meets with the stages that are doing the damage—the nymphs or larvae—and, unless it is a species with which he is familiar, it would be impossible to identify the pest, if no analytical tables were available, until the adult has been bred. It is hoped that by a careful study of the morphology and classification of immature insects, the labor of identification can be lessened.

With these facts in mind, the foregoing morphological studies have been made for the purpose of producing analytical keys to the various groups of white grubs. The author realizes their incompleteness. This is due, in great part, to the fact that many species are yet unknown, that in many instances only one or two specimens of known species are available and no extended consideration of the problem of variation can be made at this time because of the present state of our knowledge of the group. The following keys are therefore submitted as a preliminary step toward the further progress of the work. In the key to genera a few known species have been included. This key appeared in a recent paper by the writer (1928) and is here included with corrections and additions. It is gratifying to note, in view of the previously published statements that larvae of these families could not be separated, that one of Prof. J. W. McColloch's student's reports that this key, as it first appeared, has been helpful in his work with white grubs. The key to species of the genus *Phyllophaga* contains less than one-third of the known North American species of this genus, but until further progress is made with biological studies of the group little advance can be expected in our acquaintanceship with the many species now unknown in the larval stage.

LARVAL KEY TO FAMILIES OF THE SUPER-
FAMILY SCARABAEOIDEA

- 1. Posterior pair of legs small, undeveloped (Fig. 137); coxae modified into scraping, stridulating apparatus; antennae three-segmented (Fig. 94); body segments not distinctly divided into annulets and nearly devoid of spines and setae (Fig. 3) . . . PASSALIDAE, genus *Passalus*
- 1. Posterior pair of legs normally developed, legs may or may not be used for stridulation (Fig. 135, 136); antennae four or five-segmented; body segments usually distinctly divided into annulets and more or less covered with spines and setae 2
- 2. Anal segment not trilobed on cadual aspect, legs not modified for stridulation except in *Geotrupes* (Figs. 1, 12) SCARABAEIDAE
- 2. Anal segment trilobed on caudal aspect (Fig. 151, 154); meso- and metathoracic legs modified for stridation (Fig. 135, 136) 3
- 3. Labrum usually biemarginate on its distal magin, trilobed (Fig. 33, 36); emargination of peritreme of anterior spiracles on caudal margin as is the case with the remaining spiracles; anal segment strongly trilobed; larvae feed in wood (Fig. 2) LUCANIDAE
- 3. Labrum not biemarginate on its distal margin, more rounded, not trilobed on distal margin (Fig. 25); spiracular peritreme of all segments small, open on dorsal margin, poorly defined (Fig. 123); anal segment feebly trilobed (Fig. 151); larvae feed in carrion (Fig. 7) TROGIDAE, genus *Trox*

LARVAL KEY TO THE SUBFAMILIES OF SCARABAEIDAE

1. Galea and lacinia of maxilla not fused (Fig. 98, 100), that is, the mala is deeply bifid; usually coprophagous larvae..... LAPAROSTICTI 2
1. Galea and lacinia of maxilla fused to form the mala (Fig. 97, 104); mostly "leaf chafers"..... PLEUROSTICTI 6
2. Tarsi without claws (Fig. 1), a distal seta may be present; abdomen strongly "humped" on the dorsum (Fig. 1); labrum trilobed and biemarginate (Fig. 64)..... 3
2. Tarsi with claws or the tarsus is bilobed on its distal end, abdomen not "humped" on the dorsum..... 5
3. Antenna four-segmented..... COPRINAE, genus *Copris*
3. Antenna five-segmented..... 4
4. Tarsus strongly rounded or blunt on its distal end; tormae of labrum (Fig. 55, *l*) not meeting on the median line; ental setae of lateral lobes of the epipharynx (Fig. 55, *ll*) numerous (more than eight)..... COPRINAE, genus *Canthon*
4. Tarsus terminating in a long seta; tormae of labrum meeting on the median line (Fig. 67, *t*); ental setae of lateral lobes of the epipharynx scarce (usual one on each lobe)..... COPRINAE, *Onthophagus* (Fig. 4)
5. Tarsus without claws, bilobed on its distal end; posterior pair of legs considerably shortened (not as much so as in Passalidae); second and third pairs of legs modified for stridulation..... GEOTRUPINAE, genus *Geotrupes*
5. Tarsus with claws which are longer than trasus; legs not modified for stridulation; third pair of legs not noticeably shortened; body densely setaceous (Fig. 139); anal slit transverse (Fig. 139)..... GLAPHYRINAE, genus *Amphicoma*
6. Mandibles on their caudal aspect without an oval, stridulating area made up of transverse striae (Fig. 84); radula usually with two longitudinal rows of mesad pointing spines (not present in *Serica*) (Fig. 156 to 189); anal slit in the form of an obtuse angle (Fig. 156 to 189)..... MELOLONTHINAE
6. Mandibles on their caudal aspect, with a distinct oval, stridulating area made up of transverse striae (Fig. 81, *sa*); with or without two longitudinal rows of mesad pointing spines on radula; anal slit not angulate (Fig. 138) and more transverse..... 7
7. Labrum symmetrical (*Stephanucha* is not symmetrical but it is a rare species), usually trilobed (except in *Trichiotinus* which is usually recognized by the presence of ocelli): epipharynx with a conspicuous, curved row of small spines in the region of the distal sensory area (Fig. 57, *st*); dorsum of abdomen behind the last spiracle-bearing segment not divided transversely by an impressed line thus appearing as one segment (Fig. 11); some species are "black crawlers," others found in soil, wood, and manure..... CETONIINAE
7. Labrum asymmetrical, not trilobed; epipharynx without a conspicuous, curved row of small spines in the region of the distal sensory area (Fig. 42); dorsum of abdomen behind the last spiracle-bearing segment divided transversely by an impressed line making it appear as two segments (Fig. 10); species of varied habits..... 8
8. Ental aspect of the labrum with a series of transverse striae on the lateral margins at bases of lateral setae (Fig. 40, *sl*)..... Tribe Anomalini RUTELINAE
8. Ental aspect of the labrum without a series of transverse striae on the lateral margins at bases of lateral setae (Fig. 50)..... 9
9. Stridulating teeth of maxillae (Fig. 106, *ms*) sharply pointed and curved, apices directed distally (Fig. 114); distal segment of maxillary palpus usually without a distinct, setaceous sensory area..... Tribe Rutelini RUTELINAE
9. Stridulating teeth of maxilla not pointed but strongly truncate being as broad as long, not curved, and not directed distally (Fig. 124); distal tooth of the series of stridulating maxillary teeth twice as wide as the others in the series; distal segment of the maxillary palpus usually ending in a setaceous sensory area..... DYNASTINAE

LARVAL KEY TO GENERA OF SUBFAMILY MELOLONTHINAE

1. Anal slit obtusely angulate, not trilobed (Fig. 156); tarsal claws of posterior legs less than half as long as claws of the other legs; distal sensory area of epipharynx usually with seven to eight strong spines (Fig. 25). A few species of *Phyllophaga*, e.g., *lanceolata* (Fig. 26), have less than seven spines but can readily be distinguished by the lateral striae of the epipharynx. 2
1. Anal slit more acutely angulate, faintly trilobed (Fig. 140); tarsal claws of posterior legs more nearly equal in length to the claws of the other legs, never less than half as long; distal sensory area of epipharynx never with more than four strong spines (Fig. 31, *sp*). . . 3
2. Longitudinal double row of spines of radula short, scarcely more than eight spines to a row (Fig. 141); head dark brown in color; dorsum of abdominal segments very densely spinose; striations of lateral margins of epipharynx indistinct (Fig. 25); epipharynx never with a submarginal, distal row of striae *Polyphylla*
2. Longitudinal double row of spines of radula longer, usually more than ten spines to a row (Fig. 156); head light yellow in color; dorsum of abdominal segments less densely spinose; striations of lateral margins of epipharynx distinct (Fig. 26, *st*), epipharynx with a submarginal, distal row of striae, sometimes difficult to observe in some species (Fig. 26, *sms*) *Phyllophaga*
3. Epipharynx with three strong spines in distal sensory area (Fig. 31); radula with a conspicuous transverse row of spines (Fig. 140) *Serica*
3. Epipharynx with four strong spines in distal sensory area (Fig. 34) 4
4. Setae of radula not hooked at the tip; presence or absence of double longitudinal rows of spines on radula questionable;¹ Distal end of abdomen sparsely clothed with shorter, stronger setae; claws of posterior tarsi less than half as long as those of other tarsi. *Diplotaxis*
4. Setae of radula hooked at the tip (Fig. 142); radula with a short, double row of longitudinal spines; distal end of abdomen densely clothed with long delicate setae; anal opening sharply acute; claws of posterior tarsi equal in length to claws of other tarsi. *Macrodactylus*

LARVAL KEY TO GENERA OF SUBFAMILY RUTELINAE

1. Ental aspect of the labrum with a series of transverse striae on the lateral margins near bases of lateral setae (Fig. 41, *st*). Tribe ANOMALINI 2
1. Labrum without such transverse striae on its ental lateral margins (Fig. 44) Tribe RUTELINI 4
2. With two of the four spines of the distal sensory area of the epipharynx strongly fused at the base making a large spine with its distal end bifid (Fig. 52, *sp*); longitudinal, double row of spines of radula parallel, not divergent, with eight spines in the left row and nine in the right row. *Strigoderma arboricola*
2. Without two spines of the distal sensory area of the epipharynx fused at base to form a bifid spine; longitudinal double row of spines of the radula either parallel or diverging posteriorly 3
3. Radula with longitudinal rows of spines short, about seven spines in each row; rows strongly divergent posteriorly; sensilliae of distal sensory area of epipharynx at bases of distal spines about equal in size and arranged nearly semicircularly (Fig. 41) *Popillia japonica*
3. Radula with longitudinal rows of spines usually longer, with twelve to thirteen spines in each row (Fig. 143); rows more or less parallel and frequently converging posteriorly;

¹ The only specimen of "Diplotaxis" available does not show the radula distinctly. A specimen in the Illinois Natural History Survey Collection labeled "Diplotaxis" is apparently a species of *Serica*.

- sensillae of distal sensory area of epipharynx at bases of distal spines unequal in size and not arranged as definitely in a semicircle (Fig. 40, 43, 46).....*Anomala*
4. Larvae found in rotten logs or stumps, sometimes under dried manure, Labrum wider than long; with or without (Fig. 144) two longitudinal rows of spines on radula; setae of lateral margins of labrum of various lengths but not strongly curved (Fig. 44, 50).....5
4. Larvae usually formed in sandy soils, labrum (Fig. 50) as long as wide, strongly rounded but asymmetrical; without longitudinal rows of spines on radula; lateral margins of labrum with strongly curved, flattened setae which increase in length distally.....*Cotalpa lanigera*
5. Larvae found in rotten logs or stumps, without two longitudinal rows of spines on radula (Fig. 144); distal sensory area not produced into a single large, chitinous tubercle, without semicircular ring at base (Fig. 44).....*Pelidnota punctata*
5. Larvae under rotten logs or stumps, or under dried manure on sandy soils; with two longitudinal rows of spines on radula; distal sensory area of epipharynx produced into a single large chitinous tubercle, having between its base and the distal margin a narrow chitinous semicircle.....*Polymoechus brevipes*

LARVAL KEY TO GENERA OF SUBFAMILY DYNASTINAE

1. With a single ocellar spot at base of antenna.....2
1. Without an ocellar spot at base of antenna.....4
2. Radula with a longitudinal cleared area surrounded by recumbent spines similar to other spines of radula, spines not strongly differentiated as in other subfamilies having the double longitudinal row of spines; usually found in manure..*Ligyrodes (Ligyrys) relictus*
2. Radula without such a longitudinal, non-setose area formed by the absence of spines or setae.....3
3. Distal sensory area of epipharynx produced into a long, proximal pointing, chitinous process which is curved at its apex, at its base are numerous large setae (Fig. 48, *dsa*); head brownish-tan in color; usually found in burrows near manure.....*Strategus*
3. Distal sensory area of epipharynx not produced into a long, proximal pointing, chitinous process nearly devoid of setae in the region of the distal sensory area (Fig. 151); head nearly black in color, densely punctate; usually found on soil among dead leaves in woods.....*Xyloryctes*
4. Epipharynx with the chitinous portion of the distal sensory area produced to form a single broad tubercle (fig. 45); labrum strongly asymmetrical; sides of labrum strongly rounded; setae of radula very short, not hooked (Fig. 145).....*Ligyrys gibbosus*
4. Epipharynx with the chitinous portion of the distal sensory area produced to form two tubercles or spines (Fig. 53, 54), labrum more nearly symmetrical; sides of labrum less rounded.....5
5. Distal sensory area of the epipharynx produced in the form of two broad tubercles close to the distal margin of the labrum (Fig. 54); head and mandibles almost black in color; head strongly punctured; prothorax with a large, brown more heavily chitinated area on the sides which is deeply bipunctate; usually extremely large grubs.....*Dynastes tityrus*
5. Distal sensory area of the epipharynx produced in the form of two small spines and more remote from the distal margin of the labrum (Fig. 53); head yellow in color; sparsely and finely punctate; prothorax without brown, chitinous areas on sides; never extremely large grubs.....*Ochrosidia (Cyclocephala) immaculata*²

² *Dyscinetus* has not been studied. Davis (1916) states that *D. trachypygus* has "a dark brown head which is inconspicuously reticulate and covered with irregularly placed fine punctures, in this respect differing from all species (which he mentions) except *Strategus*, the head of which is much more coarsely punctate and the species is much larger. The ventral surface of the anal segment bears a patch of hooked spines and the upper surface of the same segment is covered, excepting along the median line, with fine hairs, those at the tip being shorter, stouter and more spine-like."

LARVAL KEY TO GENERA OF SUBFAMILY CETONIINAE

1. Labrum almost as long as wide, not distinctly trilobed (Fig. 66); emarginations of labrum relatively shallow; a distinct ocellar spot at base of each antenna; distal sensory area of epipharynx produced into a conspicuous chitinous tubercle; larvae live in wood. *Trichiotinus*
1. Labrum considerably wider than long, distinctly trilobed, relatively deeply emarginate (Fig. 62); no ocellar spot at base of antenna; distal sensory area not produced into a chitinous tubercle; larvae live in various situations, one genus, (*Osmoderma*,) in wood. 2
2. Epipharynx with a chitinous, semicircular carina near distal margin of the median lobe (Fig. 65); proximad of this ridge is a semicircle of about sixteen sensory pores.³ On the side of the epipharynx additional pores apparently make the semicircle continuous almost to the clypeo-labral suture; tarsal claws normal, curved and sharply pointed; larvae live in ant nests. *Cremastacheilus*
2. Epipharynx without a chitinous, semicircular carina on distal margin of median lobe; the median lobe is provided with a conspicuous semicircle of spines (Fig. 68); tarsal claws usually modified into blunt, cylindrical, setaceous tubercles⁴. 3
3. Epipharynx with about ten spines in a semicircular row in distal sensory area; placed somewhat obliquely (Fig. 68); no chitinous sensory tubercle in proximal sensory area near clypeo-labral suture mesad of tormae; larva live in sandy soil (rare). . . *Stephanucha*
3. Epipharynx usually with more than ten spines (about 15–17) in a semi-circular row in distal sensory area; placed almost transversely; with a well-defined sensory tubercle in proximal sensory area near clypeo-labral suture (Fig. 57, 59); larvae crawl on their backs. 4
4. Radula of last abdominal segment without a longitudinal, double row of mesad pointing spines; larvae live in wood. *Osmoderma eremicola*
4. Radula of last abdominal segment with a longitudinal double row of mesad pointing spines; larvae live in manure or soil that is rich in decaying organic matter. 5
5. Radula of last abdominal segment (Fig. 150) with spines of the longitudinal rows short, separated from each other by a distance nearly equal to the length of the spines; apices of opposing spines distant from each other by less than the length of an individual spine; spines about twice as long as their width at base; antepenultimate antennal segment longer than the terminal segment; usually found in rich, sandy or loam soil. . . . *Cotinis*
5. Radula of last abdominal segment (Fig. 148, 149) with spines of longitudinal rows longer, separated from each other by a distance much less than the length of the spines; apices of opposing spines separated from each other by a distance greater than the length of an individual spine; spines considerably more than twice as long as width at base; antepenultimate antennal segment not longer than the terminal segment, larvae usually found in manure. 6
6. Radula of last abdominal segment with spines of longitudinal rows diverging posteriorly (Fig. 149). *Euphoria sepulchralis*
6. Radula of last abdominal segment with spines of longitudinal rows converging posteriorly (Fig. 148). *Euphoria inda* and *Euphoria fulgida*

LARVAL KEY TO GENERA OF FAMILY LUCANIDAE

1. Antennae five-segmented. 2
1. Antennae four-segmented. 3
2. Dorsal lobe of the three anal lobes acutely pointed on its ventral margin, lateral lobes with

³ In the only specimen available for study the epipharynx is almost devoid of setae but in their place numerous pores are present which may be trichopores whose setae have been lost, or they may, in fact, be sensillia.

⁴ Claws of *Stephanucha* have not been examined.

- a concentric oval line (Fig. 154).....*Dorcus*
2. Dorsal lobe of the three anal lobes with its ventral margin strongly rounded; lateral lobes without a concentric oval line.....*Lucanus*
3. Caudal region of radula of the last ventral segment with spinose setae; anal opening on each side.....*Platycerus*⁵
3. Caudal region of radula without spinose setae (Fig. 153).....4
4. Lateral lobes of anus large, subtriangular, not emarginate at their ventral point of union; superior lobe large.....*Ceruchus*
4. Lateral lobes of anus plainly elliptical, emarginate at their ventral point of union; superior lobe small (Fig. 153).....*Sinodendron*

ARTIFICIAL KEY TO SOME KNOWN THIRD INSTAR LARVAE OF THE GENUS PHYLLOPHAGA

1. Longitudinal rows of radula with less than five spines (usually four in right and three in left row); the tips of opposing spines greatly overlapping, extending almost to the bases of the opposing spines (Southwestern species) (Fig. 157).....*cribrosa* (Lec.)
1. Longitudinal rows of radula with more than five spines in each row; the tips of opposing spines never greatly overlapping (excepting *longitarsa* which has 8 to 12 spines).....2
2. Each longitudinal row of radular spines composed of a series of spines varying from two rows at the anterior end to three and four rows posteriorly, these compound rows and space between them being rather strongly divergent posteriorly; cephalic spines usually shorter than the caudal spines (Southwestern species) (Fig. 158).....*farcta* (Lec.)
2. Each longitudinal row of radular spines composed of a single series of spines, not composed of several rows as in *farcta*, may or may not diverge posteriorly; spines of various lengths.3
3. Longitudinal rows with never more than 16 spines in each row, usually less but not fewer than five.....4
3. Longitudinal rows with more than 16 spines in a row.....10
4. Two rows of longitudinal spines arranged in the form of a distinct oval; with 12-13 spines in each row; spines short, scarcely as long as the distance separating the bases of adjoining spines (Fig. 188).....*tristis* (Fab)
4. Two rows of longitudinal spines arranged in nearly parallel rows; with from 5-16 spines in each row; spines variable in length and distance apart.....5
5. Majority of spines in each row separated from each other at base by a distance that is less than the length of the individual spines; each row of spines strongly irregular; with 8 to 16 spines in each row.....6
5. Majority of spines in each row separated from each other at base by a distance equal to, or greater than the length of the individual spines; each row of spines more nearly regular or parallel; number of spines in each row never more than 14.....7
6. Spines 14 to 16 in a row; apices of opposing spines separated by a distance equal to or slightly less than the length of the individual spines; the majority of spines directed cephalo-mesad (Fig. 163).....*gracilis* (Burm.)
6. Spines 8-12 in a row; apices of opposing spines extending beyond the meson and overlapping or crossing each other; the majority of spines directed caudo-mesad (Fig. 162).....*longitarsa* (Say)
7. Most of the apices of opposing spines separated from each other by a distance equal to or greater than the length of the individual spines; 11 to 13 spines in each row (Fig. 180).....*implicita* (Horn)
7. Most of the apices of opposing spines separated from each other by a distance less than the length of the individual spines.....8

⁵ Genus not seen. The characters given above are from Perris (1877) after Mulsant.

8. Most of the apices of opposing spines reaching the meson and very narrowly separated from each other; 12–13 spines in each row (Fig. 171) *vehemens* (Horn)
8. Most of the apices of opposing spines not reaching the meson with the opposing apices more widely separated from each other; 13–14 spines in each row 9
9. Spines shorter, much less than half the length of the distance separating the majority of adjacent spines at their base; 13 spines in each row (Fig. 156) *lanceolata* (Say)
9. Spines longer, usually greater than half the length of the distance separating the majority of adjacent spines at their base; 14 spines in each row (Fig. 175) *drakei* (Kby.)
10. Spines of radular rows not stout; individual spines usually equal in length or shorter than the intervening distance between the bases of adjacent spines; the bases of the spines much narrower than the interval between the spines 11
10. Spines of radular rows usually stout; individual spines in most instances much longer than the intervening distance between the bases of adjacent spines; in many species the bases of the spines are wider than the interval between the adjacent spines 18
11. Apices of most of the opposing spines meeting, or slightly overlapping each other, on the meson; 19–22 spines in each row; a conspicuous transverse row of setae between the radular spines and the anal opening (Fig. 161) *ephilidu* (Say)
11. Apices of most of the opposing spines not meeting on the meson, the tips of opposing spines being separated from each other by a distance equal to or greater than the length of the individual spines; 19–29 spines in each row; no conspicuous transverse row of setae between the radular spines and the anal opening 12
12. Spines of radula arranged in nearly parallel rows; 29 spines in left row, 25 in right row; spines short, scarcely longer than their width at base (Fig. 173) *horni* (Smith)
12. Spines of radular rows arranged in more irregularly parallel rows, no rows with more than 27 spines; most spines considerably longer than their width at base 13
13. Longitudinal rows with from 25 to 27 spines 14
13. Longitudinal rows with from 17 to 21 spines 15
14. Rows of spines very irregularly parallel: with 25 spines in right row and 27 in left row; spines about equal in length to the distance between adjacent bases (Fig. 189) *inversa* (Horn)
14. Rows of spines more regularly parallel; with 26 spines in each row; spines usually shorter than the distance between adjacent bases (Fig. 160) *latifrons* (Lec)
15. Radular rows of spines diverging anteriorly 16
15. Radular rows of spines not diverging anteriorly 17
16. Radular rows of spines approximate at caudal ends (distance between opposing apices of caudal spines less than the length of the spines); 19 to 20 spines in each row (Fig. 183) *delata* (Horn)
16. Radular rows of spines less approximate at caudal ends of rows (distance between opposing apices of caudal spines at least equal to or greater than the length of the spines); 17 to 19 spines in each row (Fig. 172) *fusca* (Froel.)
17. With 19 to 21 spines in each longitudinal row; the two rows constricted at middle⁶ (Fig. 176) *marginalis* (Lec.)
17. With 18 spines in each longitudinal row; the two rows not constricted at middle (Fig. 174) *fervida* (Fab.)
18. Spines of radular rows short, scarcely longer than the intervening spaces at their bases; the rows of spines strongly diverging caudally then converging near their caudal ends . . 19
18. Spines of radular rows considerably longer than the intervening spaces at their bases; not strongly divergent but in a few species becoming gradually curved near caudal ends 20

⁶ In the single third instar of this species studied this constriction appears but this may be an abnormality since several second instar grubs available do not show this constriction.

19. Spines of radular rows strongly divergent before the middle; rows not meeting at their anterior and posterior ends; with 23 spines in each row (Fig. 186).....*velula* (Horn)
19. Spines of radular rows becoming suddenly strongly divergent at or behind middle; rows meeting at anterior end; left row with a conspicuous interval devoid of spines; with 27 and 28 spines in the rows (Fig. 167).....*calceata* (Lec.)
20. Rows nearly parallel; apices of most opposing spines separated by a distance less than the length of the spines (Fig. 164).....*fulilis* (Lec.)
20. Rows more or less parallel or gradually curving; apices of the majority of opposing spines separated by a distance equal to or greater than the length of the spines.....21
21. Rows short, occupying less than half the distance between the anal opening and the anterior margin of the segment; spines regularly placed and rows slightly curving near caudal end; 20 to 22 spines per row (Fig. 187).....*affabilis* (Horn)
21. Rows longer, occupying one-half or more of the distance between the anal opening and the anterior margin of the segment; spines of varying arrangement; usually, but not always, with more than 22 spines per row.....22
22. Spines short, not more than twice as long as width at base.....23
22. Majority of spines considerably more than twice as long as width at base.....25
23. Spines of uniform size and length, rows more regularly spaced and gradually curving outward at center and approaching one another at each end; with 24 spines in one row and 29 in the other (Fig. 177).....*fraterna* Harris
23. Spines not of uniform size and length, rows more irregularly spaced and not gradually curving outward; with not less than 27 spines in any row.....24
24. Rows of spines nearly parallel, but with rather jagged rows not noticeably approaching each other at the ends; with 27 in one row and 29 in another (Fig. 165)..*prunina* (Lec.)
24. Rows of spines not parallel, slightly curving and approaching each other at caudal end; with 33 spines in one row and 32 in another (Fig. 184).....*ilicis* (Knoch)
25. Rows strongly curved anteriorly to form a rounded cephalic end composed of smaller spines, one row with 24 spines, the other with 28 spines leaving two conspicuous spines at caudal end with no spines opposing them in the other row (Fig. 185).....*crenulata* (Froel.)
25. Rows not conspicuously rounded at anterior end; without unopposed spines at caudal end of one row.....26
26. Rows of spines longer, with 32 spines in one row and 31 in the other (Fig. 179).....*profunda* (Blanch.)
26. Rows of spines shorter, with less than 30 spines in any row.....27
27. Spines irregularly placed, forming jagged rows.....28
27. Spines regularly placed, forming more even rows.....30
28. Three caudal spines of each row not more than half as long as the majority of the spines cephalad of them: with 25 spines in one row and 24 in the other (Fig. 181)..*balia* (Say)
28. Three caudal spines not differing greatly in length from the cephalic ones.....29
29. With 27 spines in each row (Fig. 166).....*congrua* (Lec.)
29. With 25 spines in one row and 26 in the other (Fig. 168).....*crassissima* (Blanch.)
30. With both rows of spines bent or constricted mesally near the middle of the rows, 29 spines in each row (Fig. 182).....*hirticula* (Knoch.)
30. With not more than one, or none, of the rows constricted near the middle of the row; not more than 26 spines in each row.....31
31. Apices of most of the opposing spines widely separated, being nearly twice the length of the spines apart.....32
31. Apices of most of the opposing spines not as widely separated, being considerably less than twice the length of the spines apart.....33
32. With the right row of spines constricted or bent near its middle; 28 spines in one row and 24 in the other (Fig. 178).....*corrosa* (Lec.)

- 32. With neither row of spines constricted or bent near the middle; 23 spines in one row and 20 in the other (Fig. 159)..... *torta* (Iec.)
- 33. Rows of spines rather regularly curved throughout; with 22 spines in one row and 25 in the other (Fig. 170)..... *micans* (Knoch)
- 33. Rows of spines somewhat bulging behind the center; with 24 spines in one row and 26 in the other (Fig. 169)..... *bipartita* (Horn)

SUMMARY

The foregoing study of the larvae of North American Lamellicornia, including the now recognized families—Scarabaeidae, Lucanidae, Trogidae, and Passalidae—attempts to bring together our knowledge of their biology, including the writer’s life-history studies, and presents keys for their identification based on morphological studies. No comparative studies of the structural characters of these insects have hitherto been attempted, and it is hoped that this work, though far from being complete, will afford a stepping-stone to further progress in our knowledge of the group.

For taxonomic purposes the characters of the mouthparts and the last abdominal segment have proved the most useful. The analytical keys can be considered only preliminary, inasmuch as a great many of our species are still unknown in the larval stage. The long life-cycle in many species makes rearing very difficult.

In the discussion given to biology, there have been brought together, in a comparative way, the more general facts concerning postembryonic development. Some consideration is given to the late embryonic processes, and larval development is considered in a general way, as is also pupal development. This is followed by more-detailed life-history studies in the sub-families Melolonthinae, Rutelinae, Dynastinae, Cetoniinae, and the coprophagous species of the family Scarabaeidae.

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PLATE I

EXPLANATION OF PLATE I

LATERAL ASPECTS OF THE LARVAE OF SCARABAEOIDEA

- Fig. 1. *Pinotus carolina*.
Fig. 2. *Sinodendron rugosum*.
Fig. 3. *Passalus cornutus*.
Fig. 4. *Onthophagus vaca* (after Mulsant).
Fig. 5. *Amphicoma* sp.
Fig. 6. *Aphodius* sp. (probably *fimetarius*).

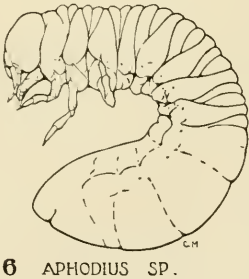
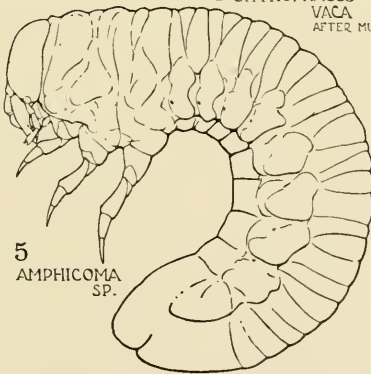
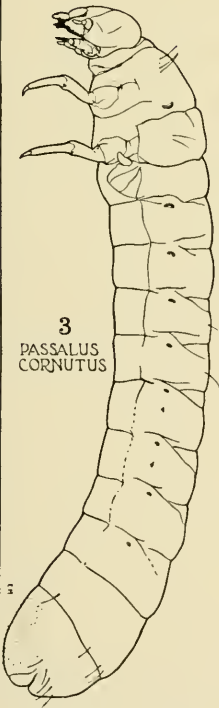
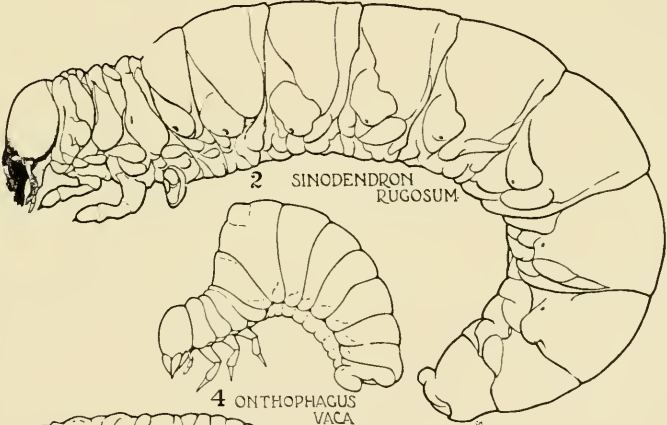
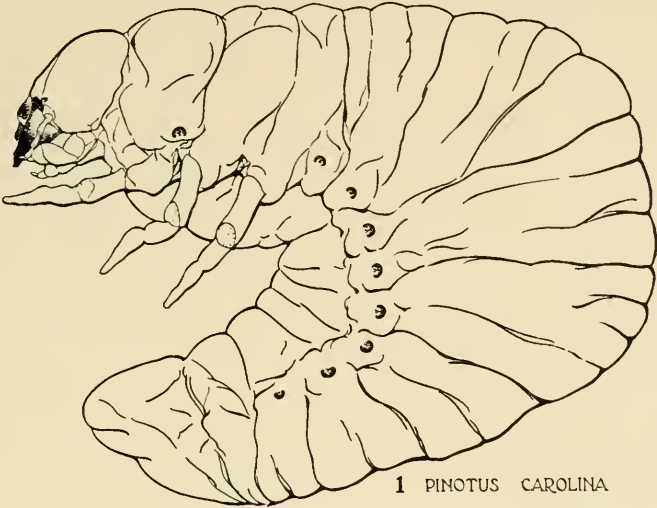


PLATE II

EXPLANATION OF PLATE II
LATERAL ASPECTS OF THE LARVAE OF SCARABAEOIDEA

- Fig. 7. *Trox* sp.
Fig. 8. *Anomala kansana*.
Fig. 9. *Ochrosidia immaculata*.
Fig. 10. *Ligyryus gibbosus*.
Fig. 11. *Euphoria inda*.
Fig. 12. *Phyllophaga crassissima*.

ABBREVIATIONS EMPLOYED

<i>ant</i>	antenna	<i>pc</i>	preclypeus
<i>as</i>	anal slit	<i>pse</i>	postclypeus
<i>es</i>	epicranial suture	<i>r</i>	radula
<i>f</i>	front	I	prothorax
<i>l</i>	labrum	II	mesothorax
<i>md</i>	mandible	III	metathorax
<i>mp</i>	maxillary palpus	1-10	abdominal segments

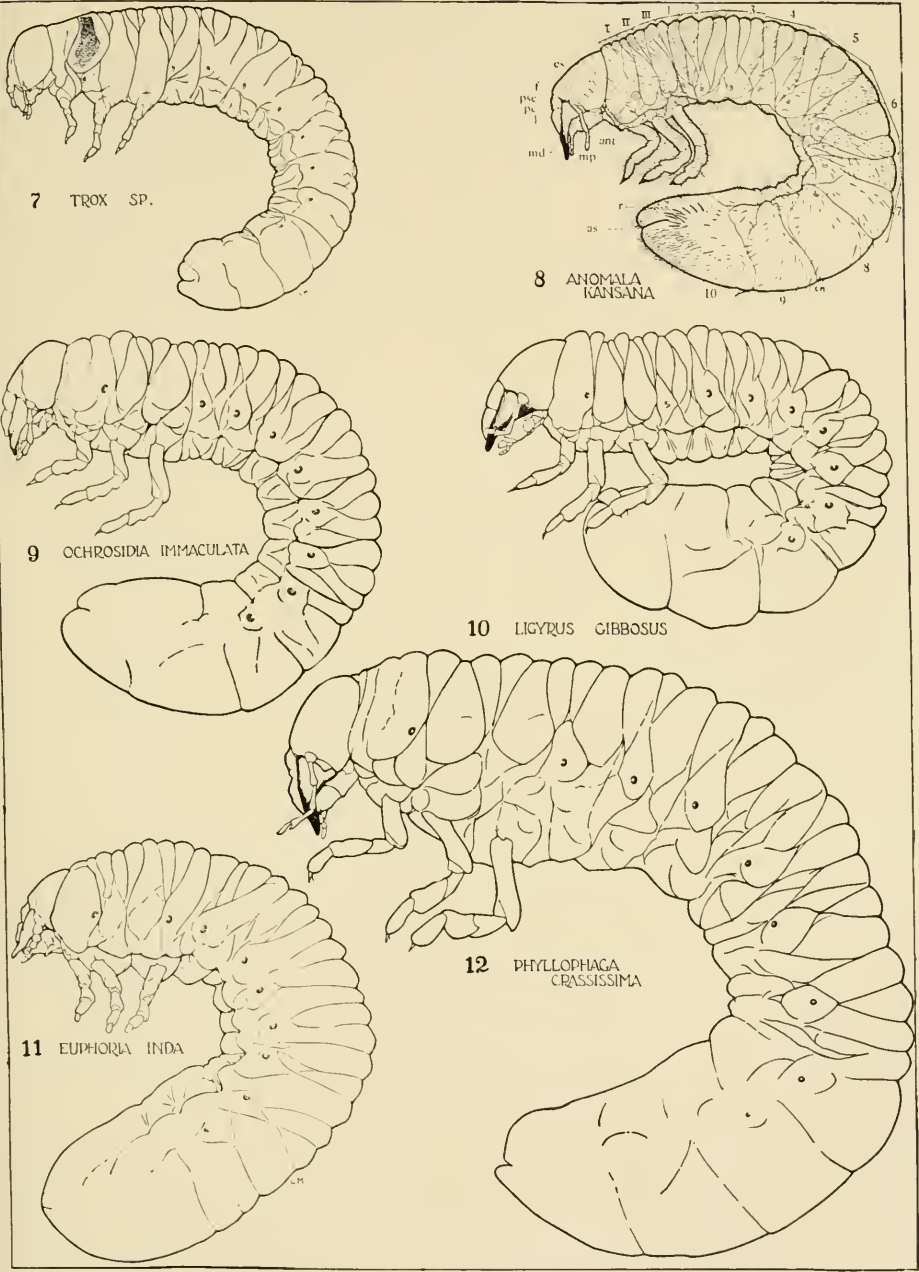


PLATE III

EXPLANATION OF PLATE III
CEPHALIC ASPECT OF THE LARVAL HEADS

- Fig. 13. *Canthon laevis*.
Fig. 14. *Aphodius* sp.
Fig. 15. *Amphicoma* sp.
Fig. 16. *Phyllophaga crassissima*.
Fig. 17. *Serica* sp.
Fig. 18. *Anomala kansana*.
Fig. 19. *Ligyris gibbosus*.
Fig. 20. *Cotalpa lanigera*.
Fig. 21. *Euphoria inda*.
Fig. 22. *Trox* sp.
Fig. 23. *Sinodendron rugosum*.
Fig. 24. *Passalus cornutus*.

ABBREVIATIONS EMPLOYED

<i>ant</i>	antenna	<i>md</i>	mandible
<i>ea</i>	epicranial arm	<i>pc</i>	preclypeus
<i>es</i>	epicranial suture	<i>pcl</i>	precoilla
<i>f</i>	front	<i>pse</i>	postclypeus
<i>fcs</i>	fronto-clypeal suture	<i>v</i>	vertex
<i>l</i> or <i>lab</i>	labrum		

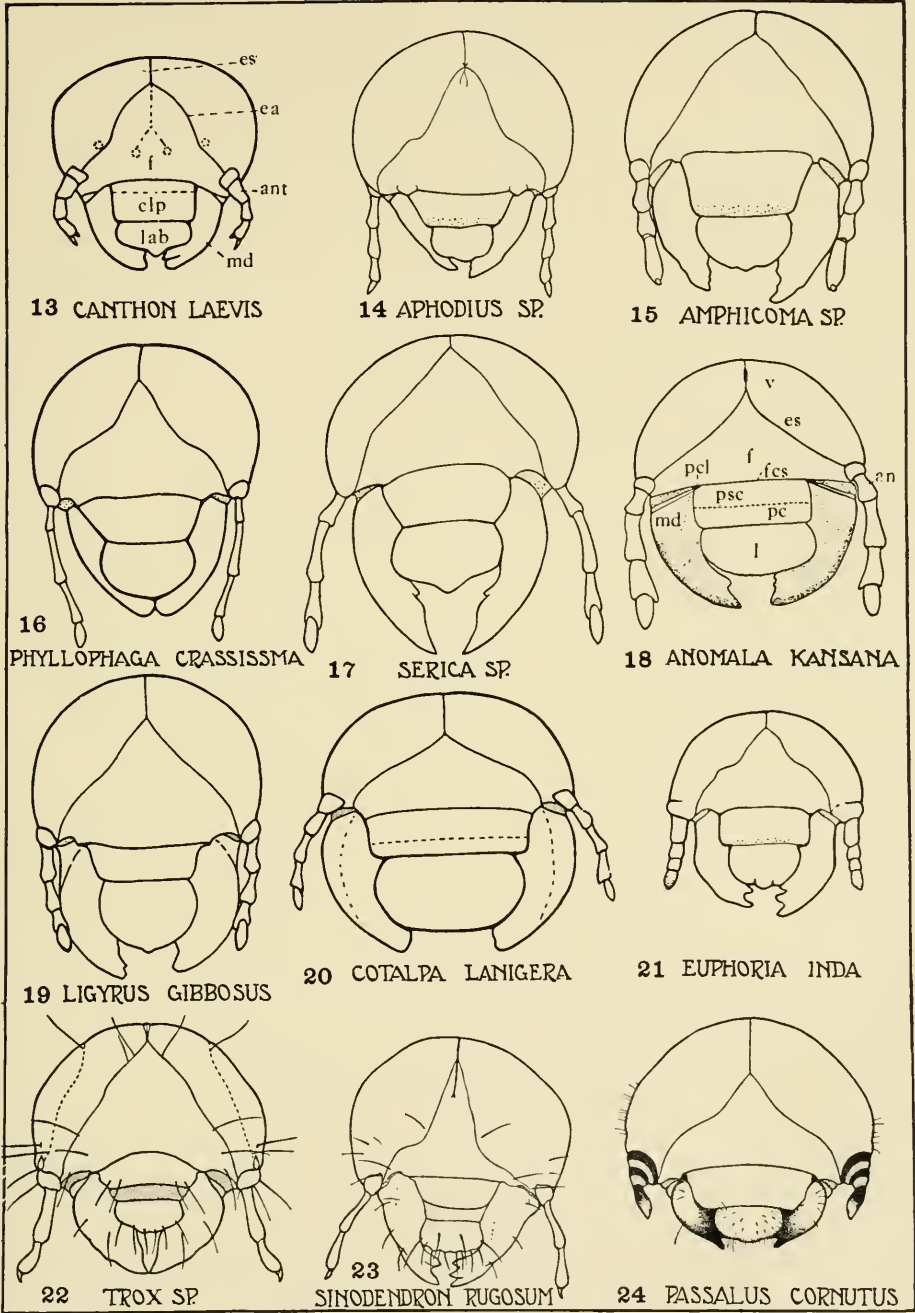


PLATE IV

EXPLANATION OF PLATE IV

EPIPHARYNX

- Fig. 25. *Polyphylla decemlineata*.
 Fig. 26. *Phyllophaga lanceolata*.
 Fig. 27. *Phyllophaga tristis*.
 Fig. 28. *Macroductylus subspinosus*.
 Fig. 29. *Phyllophaga fusca*.
 Fig. 30. *Dorcus* sp.
 Fig. 31. *Serica* sp.
 Fig. 32. *Phyllophaga rugosa*.
 Fig. 33. *Sinodendron rugosum*.
 Fig. 34. *Diplotaxis* sp.
 Fig. 35. *Phyllophaga cribrata*.
 Fig. 36. *Passalus cornutus*.
 Fig. 37. *Phyllophaga futilis*.
 Fig. 38. *Phyllophaga corrosa*.
 Fig. 39. *Trox* sp.

ABBREVIATIONS EMPLOYED

<i>cp</i>	chitinous plate	<i>psa</i>	proximal sensory area
<i>cls</i>	clypeal sensillia	<i>sa</i>	sensillia
<i>clst</i>	clypeo-labral suture	<i>sc</i>	sense cone
<i>dsa</i>	distal sensory area	<i>sms</i>	submarginal striae
<i>ll</i>	lateral lobe	<i>sp</i>	spines
<i>ls</i>	lateral striae	<i>st</i>	setae
<i>ml</i>	median lobe	<i>t</i>	torma

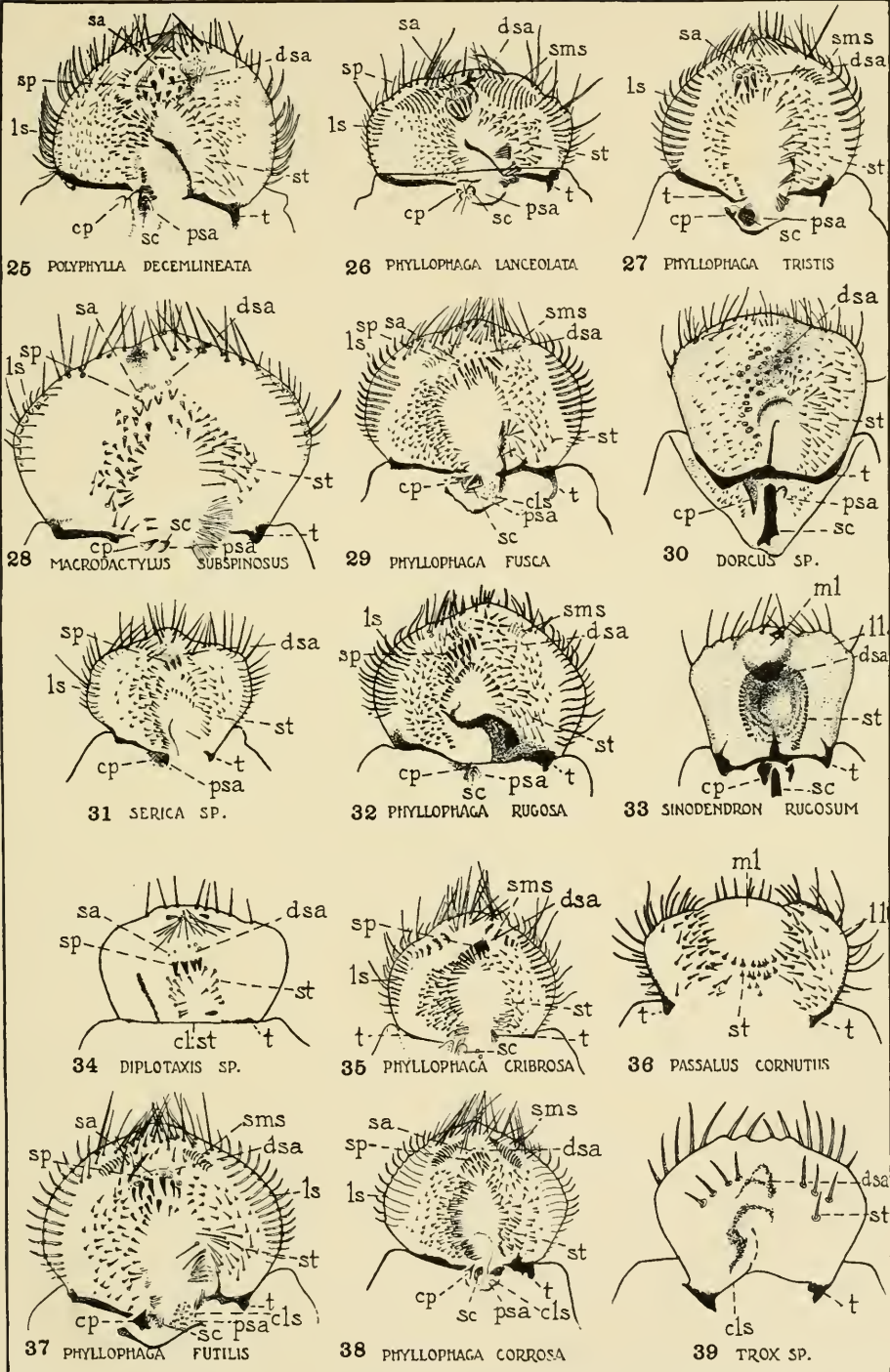


PLATE V

EXPLANATION OF PLATE V

EPIPHARYNX

- Fig. 40. *Anomala orientalis*.
 Fig. 41. *Popillia japonica*.
 Fig. 42. *Ligyrodes relictus*.
 Fig. 43. *Anomala kansana*.
 Fig. 44. *Pelidnota punctata*.
 Fig. 45. *Ligyryus gibbosus*.
 Fig. 46. *Anomala innuba*.
 Fig. 47. *Polymoechus brevipēs*.
 Fig. 48. *Strategus antaeus*.
 Fig. 49. *Anomala binotata*.
 Fig. 50. *Cotalpa lanigera*.
 Fig. 51. *Xyloryctes satyrus*.
 Fig. 52. *Strigoderma arboricola*.
 Fig. 53. *Ochrosidia immaculata*.
 Fig. 54. *Dynastes tityrus*.

ABBREVIATIONS EMPLOYED

<i>cp</i>	chitinous plate	<i>psa</i>	proximal sensory area
<i>cls</i>	clypeal sensillia	<i>sa</i>	sensillia
<i>clst</i>	clypeo-labral suture	<i>sc</i>	sense-cone
<i>dsa</i>	distal sensory area	<i>sms</i>	submarginal striae
<i>ll</i>	lateral lobe	<i>sp</i>	spines
<i>ls</i>	lateral striae	<i>st</i>	setae
<i>ml</i>	median lobe	<i>+</i>	torma

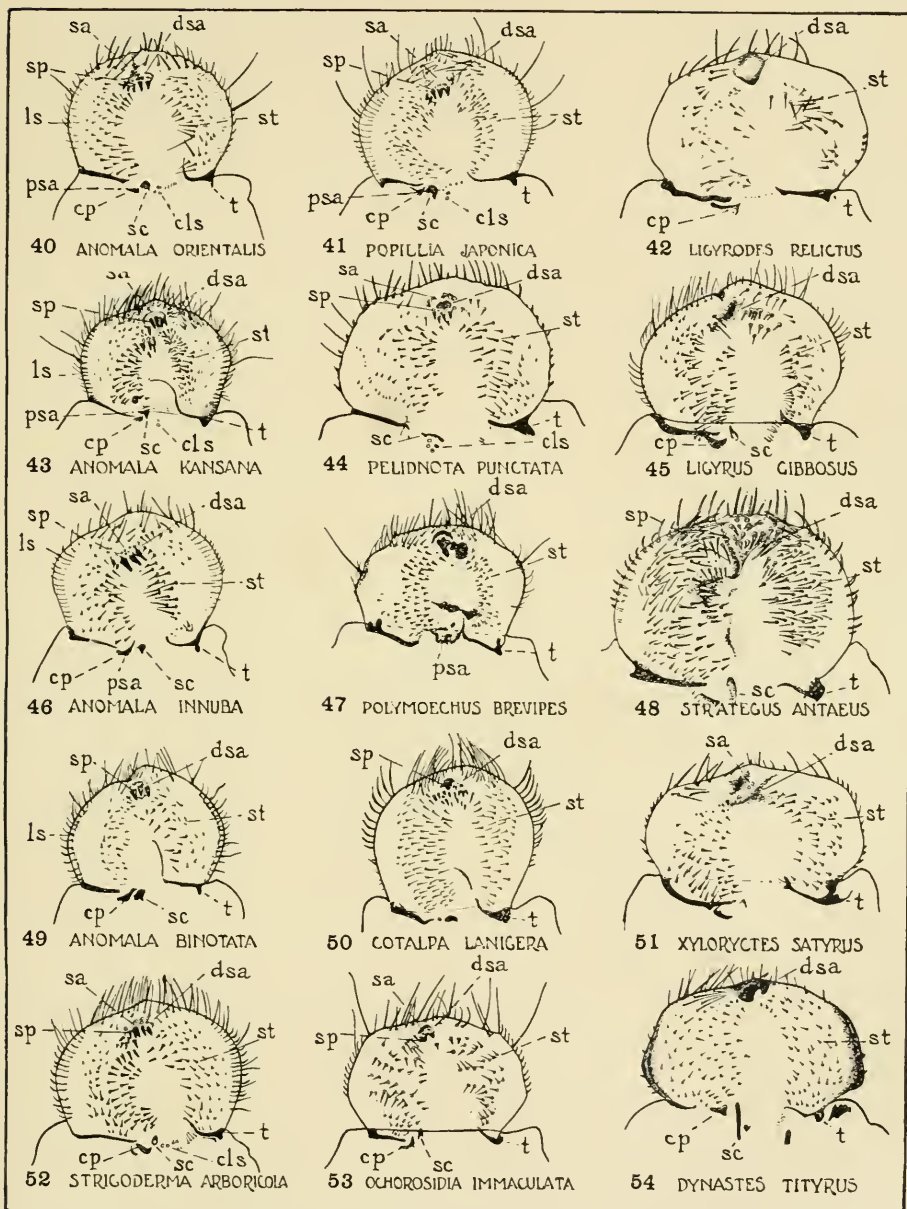


PLATE VI

EXPLANATION OF PLATE VI

EPIPHARYNX

- Fig. 55. *Canthon laevis*.
 Fig. 56. *Aphodius* sp.
 Fig. 57. *Euphoria fulgida*.
 Fig. 58. *Geotrupes stercorarius*. (after Schiödte)
 Fig. 59. *Cotinis nitida*.
 Fig. 60. *Euphoria sepulchralis*.
 Fig. 61. *Amphicoma* sp.
 Fig. 62. *Osmoderma eremicola*.
 Fig. 63. *Euphoria inda*.
 Fig. 64. *Copris tullius*.
 Fig. 65. *Cremastocheilus* sp.
 Fig. 66. *Trichiotinus piger*.
 Fig. 67. *Onthophagus* sp.
 Fig. 68. *Stephanucha pilipennis*.
 Fig. 69. *Phyllophaga futilis*. sense cone

ABBREVIATIONS EMPLOYED

<i>cp</i>	chitinous plate	<i>psa</i>	proximal sensory area
<i>cls</i>	clypeal sensillia	<i>sa</i>	sensillia
<i>clst</i>	clypeo-labral suture	<i>sc</i>	sense-cone
<i>dsa</i>	distal sensory area	<i>sms</i>	submarginal striae
<i>ll</i>	lateral lobe	<i>sp</i>	spines
<i>ls</i>	lateral striae	<i>st</i>	setæ
<i>ml</i>	median lobe		torma

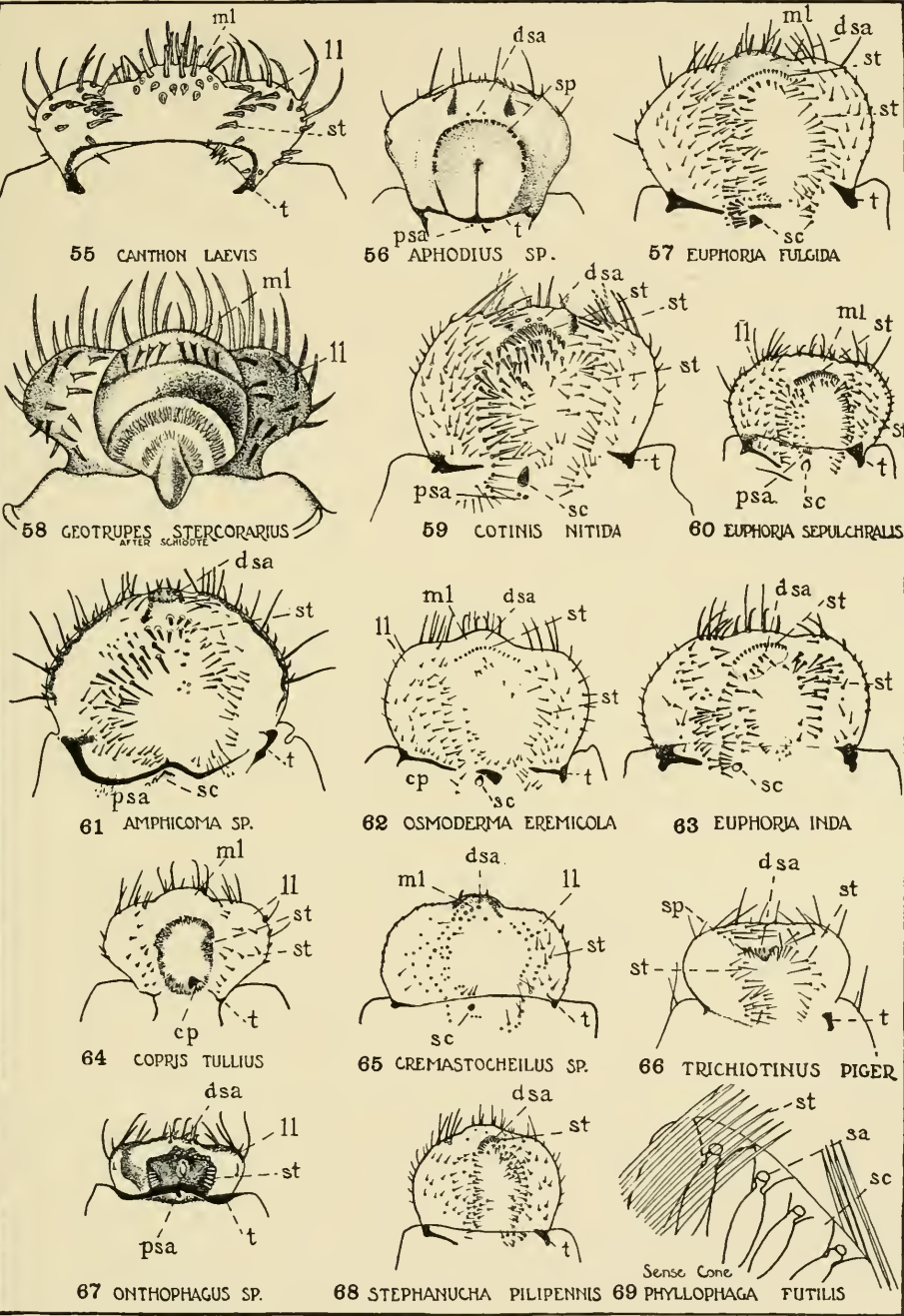


PLATE VII

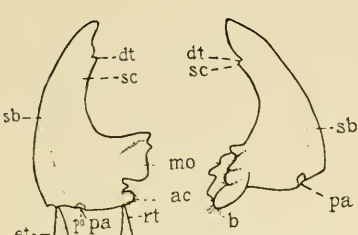
EXPLANATION OF PLATE VII

RIGHT AND LEFT MANDIBLES.—CEPHALIC ASPECT

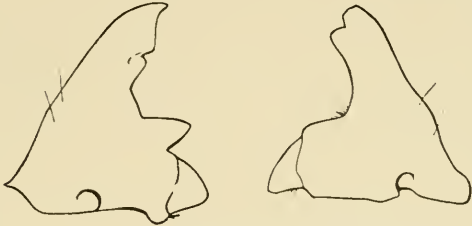
- Fig. 70. *Anomala kansana*.
 Fig. 71. *Aphodius fimetarius*.
 Fig. 72. *Stephanucha pilipennis*.
 Fig. 73. *Euphoria inda*.
 Fig. 74. *Cotalpa lanigera*.
 Fig. 75. *Ligyryus gibbosus*.
 Fig. 76. *Phyllophaga crassissima*.
 Fig. 77. Mandibular articulation.
 Fig. 78. *Canthon laevis*.
 Fig. 79. *Passalus cornutus*.
 Fig. 80. *Sinodendron rugosum*.

ABBREVIATIONS EMPLOYED

<i>ac</i>	acia	<i>pa</i>	preartis
<i>b</i>	brustia	<i>pcl</i>	precoila
<i>dt</i>	dentes	<i>rt</i>	rectotendon
<i>et</i>	extensotendon	<i>sb</i>	scrobe
<i>mo</i>	molar area	<i>sc</i>	scissorial area



70 ANOMALA KANSANA



71 APHODIUS FIMETARIUS



72 STEPHANUCHA PILIPENNIS



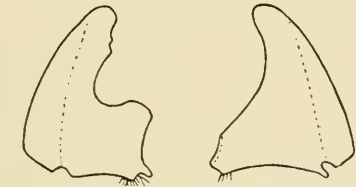
73 EUPHORIA INDA



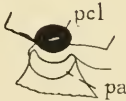
74- COTALPA LANIGERA



75- LIGYRUS GIBBOSUS



76 PHYLLOPHAGA CRASSISSIMA



77 MANDIBULAR
ARTICULATION



78 CANTHON LAEVIS



79 PASSALUS CORNUTUS



80 SINODENDRON RUGOSUM

PLATE VIII

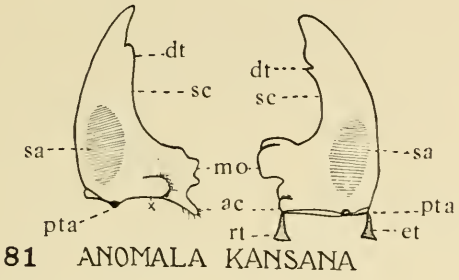
EXPLANATION OF PLATE VIII

RIGHT AND LEFT MANDIBLES—CAUDAL ASPECT AND EPIPHARYNX

- Fig. 81. *Anomala kansana*.
 Fig. 82. *Euphoria inda*.
 Fig. 83. *Cotalpa lanigera*.
 Fig. 84. *Phyllophaga crassissima*.
 Fig. 85. *Canthon laevis*.
 Fig. 86. *Amphicoma* sp.
 Fig. 87. *Stephanucha pilipennis*.
 Fig. 88. *Ligyris gibbosus*.
 Fig. 89. *Passalus cornutus*.
 Fig. 90. *Pinotus carolina*. Epipharynx.
 Fig. 91. *Anomala kansana*. Showing connection of epipharynx and hypopharynx.

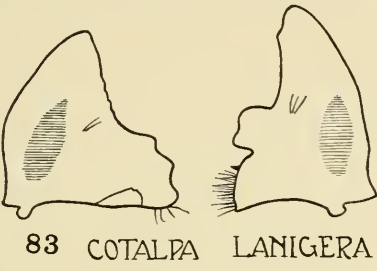
ABBREVIATIONS EMPLOYED

<i>ac</i>	acia	<i>pc</i>	precoila
<i>cl</i>	clypeus	<i>pta</i>	postartis
<i>dt</i>	dentes	<i>rt</i>	rectotendon
<i>et</i>	extensotendon	<i>sa</i>	stridulating area
<i>hc</i>	hypopharyngeal chitization	<i>sc</i>	scissorial area
<i>mo</i>	molar area	<i>t</i>	torma



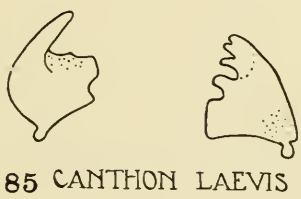
81 ANOMALA KANSANA

82 EUPHORIA INDA



83 COTALPA LANIGERA

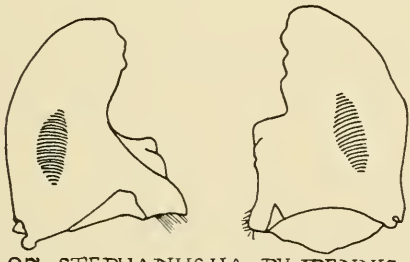
84 P. CRASSISSIMA



85 CANTHION LAEVIS



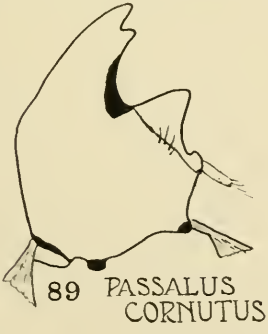
86 AMPHICOMA SP.



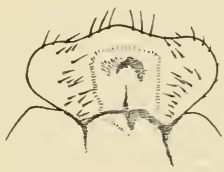
87 STEPHANUCHA PILIPENNIS



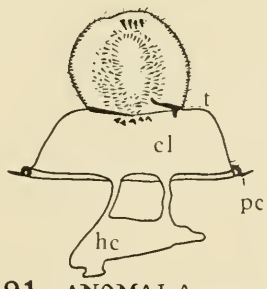
88 LIGYRUS GIBBOSUS



89 PASSALUS CORNUTUS



90 PINOTUS CAROLINA



91 ANOMALA KANSANA

PLATE IX

EXPLANATION OF PLATE IX

CAUDAL AND LATERAL ASPECTS OF HEAD; ANTENNAE, MAXILLAE AND PARTS, SPIRACLES, LEGS

- Fig. 92. *Phyllophaga crassissima*. Caudal aspect of the head.
 Fig. 93. *Canthon laevis*. Caudal aspect of the head.
 Fig. 94. *Passalus cornutus*. Antenna.
 Fig. 95. *Stephanucha pilipennis*. Antenna.
 Fig. 96. *Anomala kansana*. Antenna.
 Fig. 97. *Ligyris gibbosus*. Cephalic aspect of right maxilla.
 Fig. 98. *Canthon laevis*. Cephalic aspect of right maxilla.
 Fig. 99. *Amphicoma* sp. Cephalic aspect of right maxilla.
 Fig. 100. *Aphodius* sp. Cephalic aspect of right maxilla.
 Fig. 101. *Anomala kansana*. Prothoracic leg.
 Fig. 102. *Anomala kansana*. Metathoracic leg.
 Fig. 103. *Passalus cornutus*. Cephalic aspect of right maxilla.
 Fig. 104. *Stephanucha pilipennis*. Cephalic aspect of right maxilla.
 Fig. 105. *Anomala kansana*. Caudal aspect of right maxilla.
 Fig. 106. *Anomala kansana*. Cephalic aspect of right maxilla.
 Fig. 107. *Anomala kansana*. Articulation of maxilla and postgena.
 Fig. 108. *Anomala kansana*. Lateral aspect of the head.
 Fig. 109. Articulation of mandible and maxillae with head capsule.
 Fig. 110. *Anomala kansana*. Labrum.
 Fig. 111. *Amphicoma* sp. Stridulating teeth of right maxilla.
 Fig. 112. *Anomala kansana*. Stridulating tooth of left maxilla.
 Fig. 113. *Anomala kansana*. Stridulating teeth of right maxilla.
 Fig. 114. *Cotalpa lanigera*. Stridulating teeth of right maxilla.
 Fig. 115. *Ligyris gibbosus*. Mesal aspect of fused galea and lacinia.
 Fig. 116. *Cotalpa lanigera*. Mesal aspect of fused galea and lacinia.
 Fig. 117. *Canthon laevis*. Mesal aspect of divided galea and lacinia.
 Fig. 118. *Phyllophaga crassissima*. Stridulating teeth of right maxilla.
 Fig. 119. *Canthon laevis*. Stridulating teeth of right maxilla.
 Fig. 120. *Euphoria inda*. Mesal aspect of fused galea and lacinia.
 Fig. 121. *Phyllophaga crassissima*. Mesal aspect of fused galea and lacinia.
 Fig. 122. *Anomala kansana*. Left prothoracic spiracle.
 Fig. 123. *Trox* sp. Left prothoracic spiracle.
 Fig. 124. *Ligyris gibbosus*. Stridulating teeth of right maxilla.
 Fig. 125. *Euphoria inda*. Stridulating teeth of right maxilla.

ABBREVIATIONS EMPLOYED

<i>ac</i>	alacardo	<i>of</i>	occipital foramen
<i>ant</i>	antenna	<i>opg</i>	occipito-postgenal suture
<i>cd</i>	cardo	<i>pa</i>	preartitis
<i>cl</i>	claw	<i>pc</i>	preclypeus
<i>cx</i>	coxa	<i>pcl</i>	precoila
<i>cs</i>	epicranial suture	<i>pf</i>	palpifer
<i>f</i>	front	<i>pg</i>	postgena
<i>fm</i>	femur	<i>pra</i>	parartis
<i>g</i>	gena	<i>prc</i>	paracoila
<i>l</i>	labrum	<i>ps</i>	parastipes or subgalea
<i>lc</i>	labacoria	<i>pse</i>	postclypeus
<i>lp</i>	labial palpus	<i>pta</i>	postartis
<i>m</i>	mala	<i>ptc</i>	postcoila
<i>md</i>	mandible	<i>s</i>	stipes
<i>mld</i>	maxillaria or maxillary pleurite	<i>sc</i>	subcardo
<i>mp</i>	maxillary palpus	<i>sm</i>	submentum
<i>ms</i>	maxillary scraper	<i>st</i>	stridulating tooth
<i>mt</i>	mentum	<i>th</i>	terbio-tarsus
<i>mx</i>	maxilla	<i>tr</i>	trochanter
<i>oc</i>	occiput	<i>v</i>	vertex

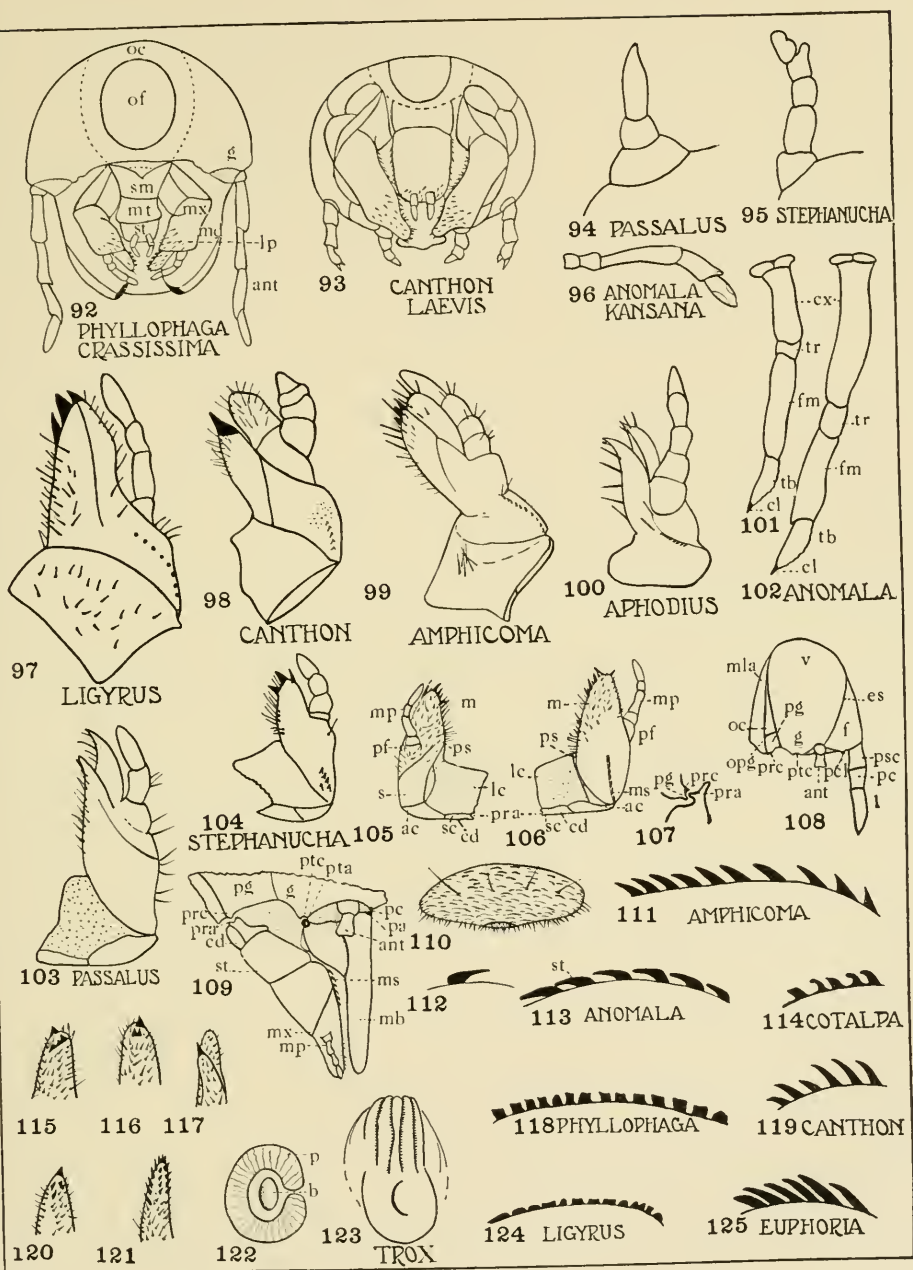


PLATE X

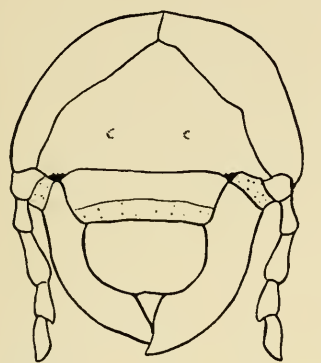
EXPLANATION OF PLATE X

CEPHALIC ASPECT OF HEAD; HYPOPHARYNX, STRIDULATING LEGS

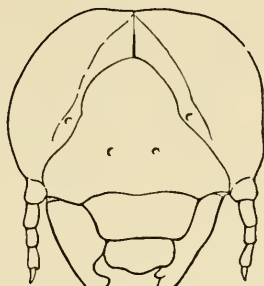
- Fig. 126. *Ochrosidia (Cyclocephala) immaculata*. Cephalic aspect of the head.
 Fig. 127. *Pinotus (Copriss) carolina*. Cephalic aspect of the head.
 Fig. 128. *Cotalpa lanigera*. Hypopharynx.
 Fig. 129. *Euphoria inda*. Hypopharynx.
 Fig. 130. *Canthon laevis*. Hypopharynx.
 Fig. 131. *Phyllophaga crassissima*. Hypopharynx.
 Fig. 132. *Ligyris gibbosus*. Hypopharynx.
 Fig. 133. *Anomala kansana*. Hypopharynx and mandibles showing their relation to each other.
 Fig. 134. *Anomala kansana*. Hypopharynx with pharynx attached.
 Fig. 135. *Ceruchus piceus*. Metathoracic leg showing stridulating surface on the trochanter.
 Fig. 136. *Ceruchus piceus*. Mesothoracic leg showing stridulating surface on the coxa.
 Fig. 137. *Passalus cornutus*. Meso- and metathoracic legs showing the stridulating modification.

ABBREVIATIONS EMPLOYED

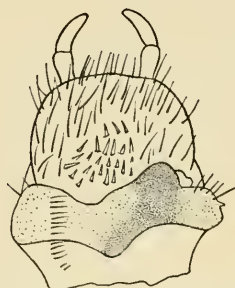
<i>cx</i>	coxa	<i>mtl</i>	metathoracic leg
<i>fm</i>	femur	<i>ph</i>	pharynx
<i>hc</i>	hypopharynx	<i>pta</i>	postcolla
<i>md</i>	mandible	<i>tt</i>	tibio-tarsus
<i>msc</i>	mesothoracic leg	<i>tr</i>	trochanter



126 OCHROSIDIA IMMACULATA



127 PINOTUS CAROLINA



128 COTALPA LANIGERA



129 EUPHORIA INDA



130 CANTHON
LAEVIS



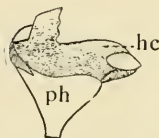
131 PHYLLOPHAGA
CRASSISSIMA



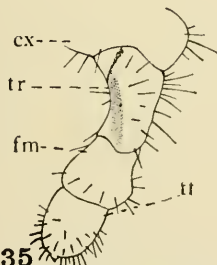
132 LIGYRUS GIBBOSUS



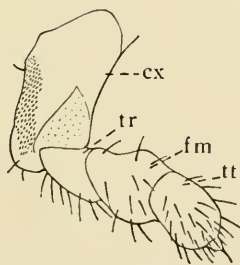
133 HYPOPHARYNX
AND MANDIBLES



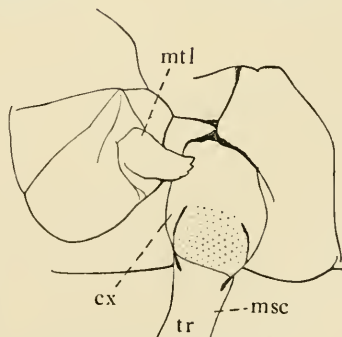
134 HYPOPHARYNX
AND PHARYNX



135 CERUCHUS PICEUS



136 CERUCHUS PICEUS



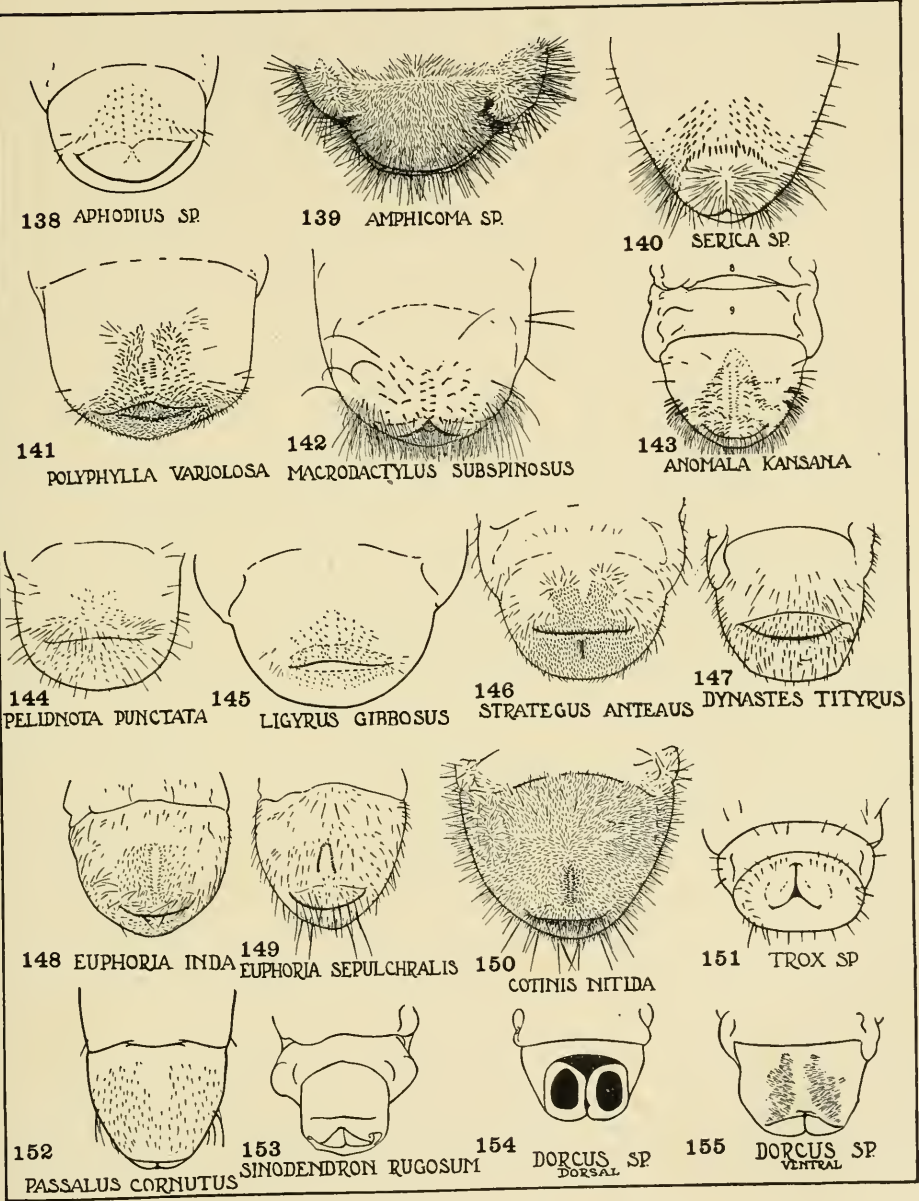
137 PASSALUS CORNUTUS

PLATE XI

EXPLANATION OF PLATE XI

RADULA OF LAST VENTRAL ABDOMINAL SEGMENT

- Fig. 138. *Aphodius* sp.
Fig. 139. *Amphicoma* sp.
Fig. 140. *Serica* sp.
Fig. 141. *Polyphylla variolosa*.
Fig. 142. *Macroductylus subspinosus*.
Fig. 143. *Anomala kansana*.
Fig. 144. *Pelidnota punctata*.
Fig. 145. *Ligyris gibbosus*.
Fig. 146. *Strategus anteaues*.
Fig. 147. *Dynastes tityrus*.
Fig. 148. *Euphoria inda*.
Fig. 149. *Euphoria sepulchralis*.
Fig. 150. *Cotinis nitida*.
Fig. 151. *Trox* sp.
Fig. 152. *Passalus cornutus*.
Fig. 153. *Sinodendron rugosum*.
Fig. 154. *Dorcus* sp. (Dorsal).
Fig. 155. *Dorcus* sp. (Ventral).



EXPLANATION OF PLATE XII

RADULA OF LAST VENTRAL ABDOMINAL SEGMENT IN PHYLLOPHAGA

- Fig. 156. *Phyllophaga lanceolata*.
Fig. 157. *Phyllophaga cribrosa*.
Fig. 158. *Phyllophaga farcta*.
Fig. 159. *Phyllophaga torta*.
Fig. 160. *Phyllophaga latifrons*.
Fig. 161. *Phyllophaga ephilida*.
Fig. 162. *Phyllophaga longitarsa*.
Fig. 163. *Phyllophaga gracilis*.
Fig. 164. *Phyllophaga futilis*.
Fig. 165. *Phyllophaga prunina*.
Fig. 166. *Phyllophaga congrua*.
Fig. 167. *Phyllophaga calceata*.

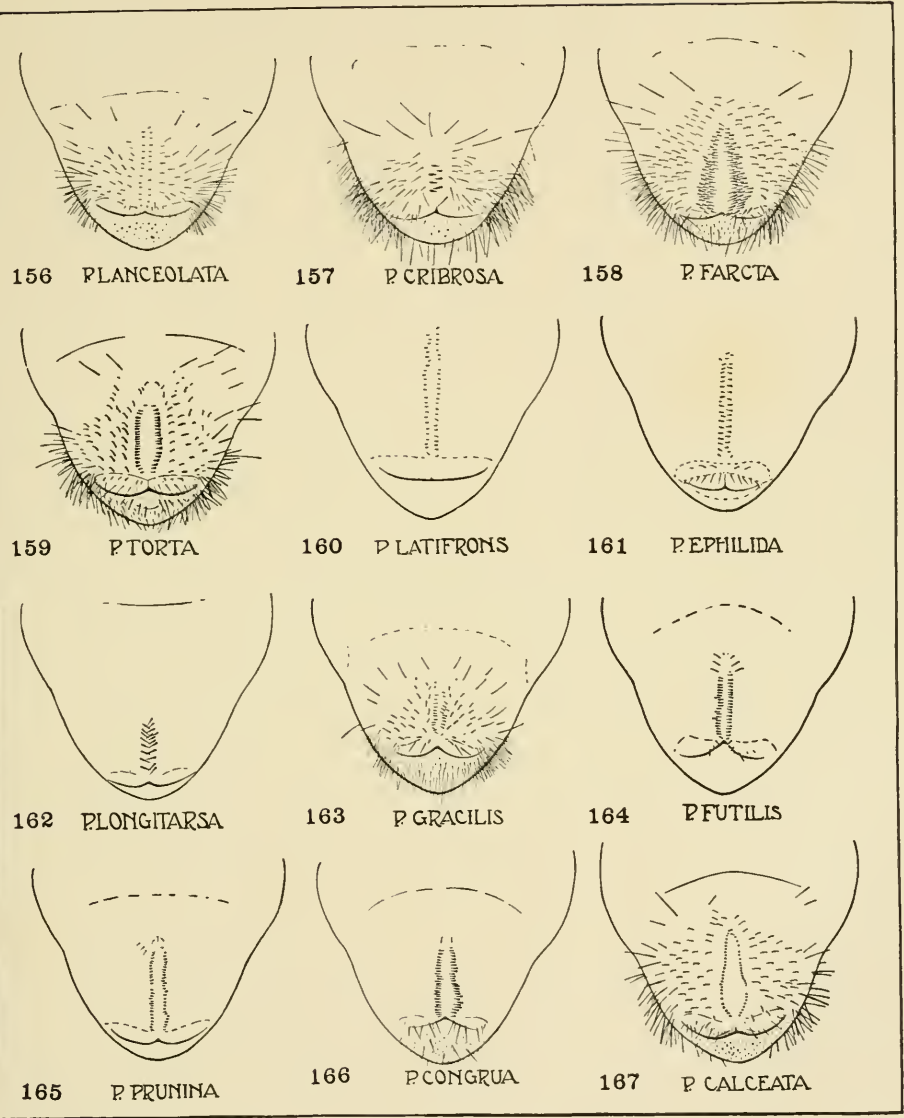


PLATE XIII

EXPLANATION OF PLATE XIII

RADULA OF LAST VENTRAL ABDOMINAL SEGMENT IN PHYLLOPHAGA

- Fig. 168. *Phyllophaga crassissima*.
Fig. 169. *Phyllophaga bipartita*.
Fig. 170. *Phyllophaga micans*.
Fig. 171. *Phyllophaga vehemens*.
Fig. 172. *Phyllophaga fusca*.
Fig. 173. *Phyllophaga horni*.
Fig. 174. *Phyllophaga fervida*.
Fig. 175. *Phyllophaga drakei*.
Fig. 176. *Phyllophaga marginalis*.
Fig. 177. *Phyllophaga fraterna*.
Fig. 178. *Phyllophaga corrosa*.
Fig. 179. *Phyllophaga profunda*.

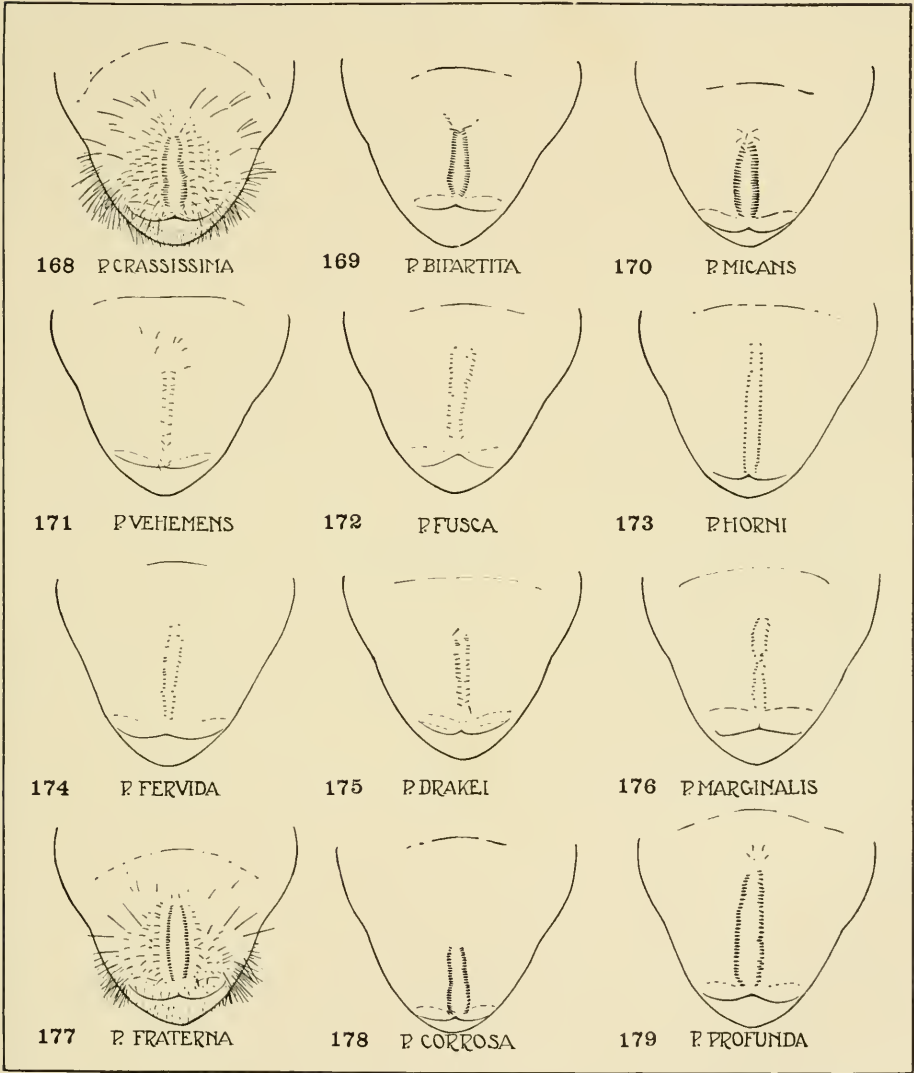


PLATE XIV

EXPLANATION OF PLATE XIV

RADULA OF LAST VENTRAL ABDOMINAL SEGMENT IN PHYLLOPHAGA, OCHROSIDIA, AND PINOTUS

- Fig. 180. *Phyllophaga implicita*.
Fig. 181. *Phyllophaga balia*.
Fig. 182. *Phyllophaga hirticula*.
Fig. 183. *Phyllophaga delata*.
Fig. 184. *Phyllophaga ilicis*.
Fig. 185. *Phyllophaga crenulata*.
Fig. 186. *Phyllophaga vetula*.
Fig. 187. *Phyllophaga affabilis*.
Fig. 188. *Phyllophaga tristis*.
Fig. 189. *Phyllophaga inversa*.
Fig. 190. *Ochrosidia immaculata*.
Fig. 191. *Pinotus carolina*.

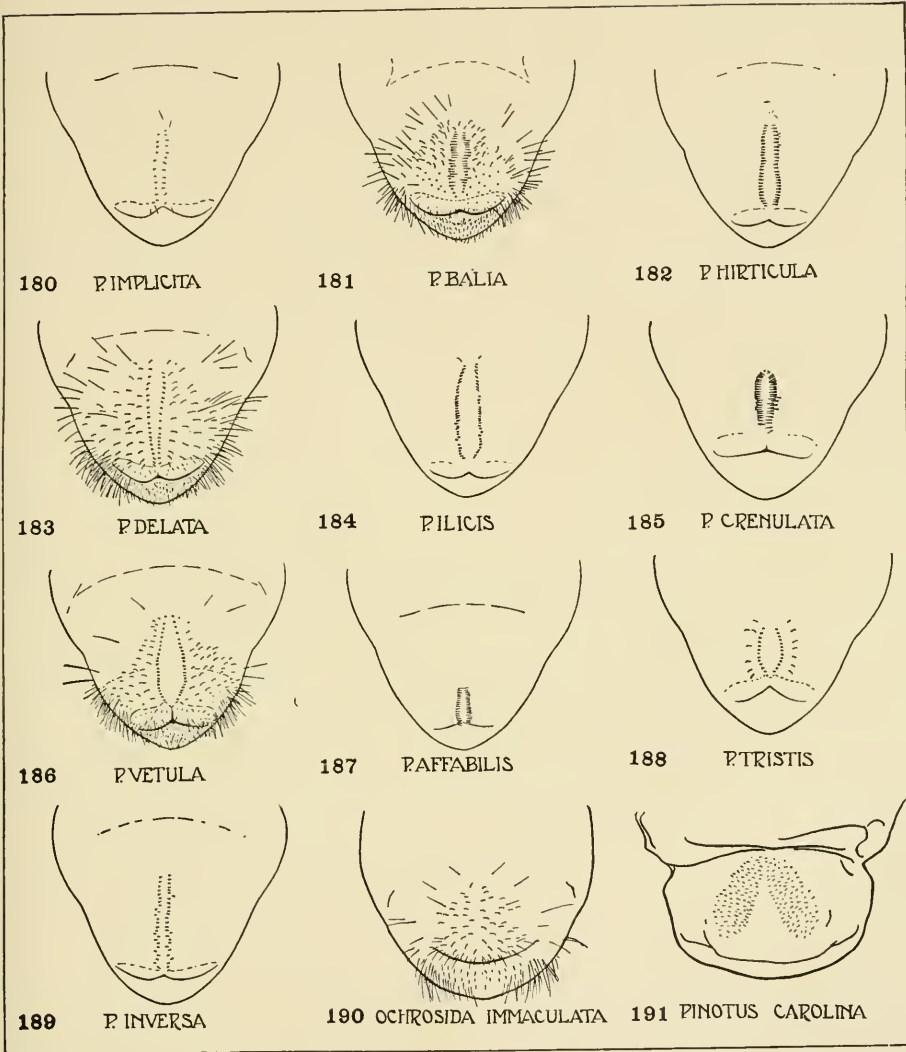


PLATE XV

EXPLANATION OF PLATE XV

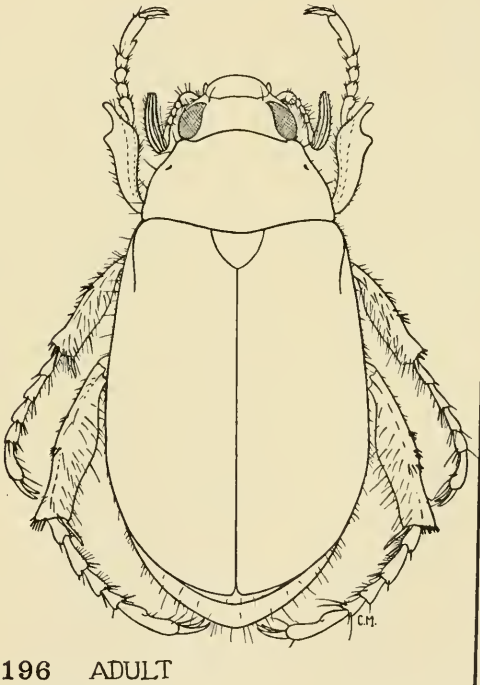
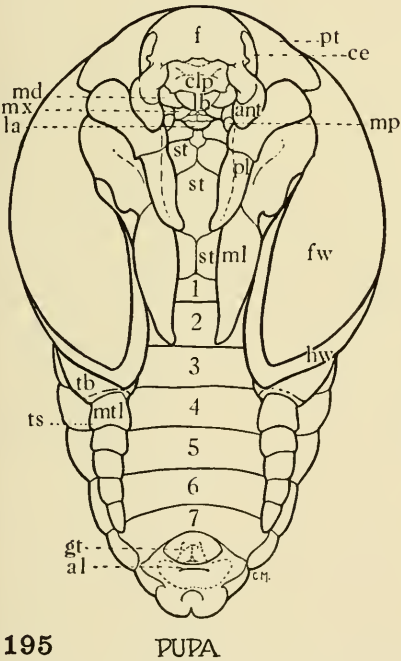
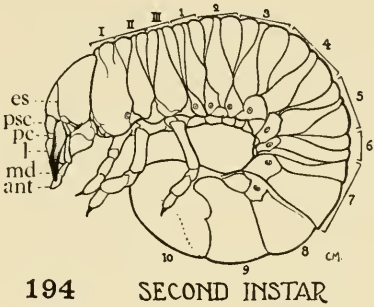
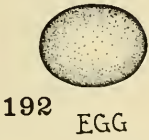
LIFE STAGES AND INSTARS OF A TYPICAL SCARABAEID, *Anomala kansana*
(For third instar of this species see figure 8, Plate II)

- Fig. 192. Egg stage.
Fig. 193. First larval instar.
Fig. 194. Second larval instar.
Fig. 195. Pupal stage.
Fig. 196. Adult stage.

ABBREVIATIONS EMPLOYED

<i>al</i> anal slit	<i>md</i> mandible
<i>ant</i> antenna	<i>ml</i> mesothoracic leg
<i>ce</i> compound eye	<i>mp</i> maxillar palpus
<i>clp</i> clypeus	<i>mtl</i> metathoracic leg
<i>es</i> epicranial suture	<i>mx</i> maxilla
<i>f</i> front	<i>pc</i> preclypeus
<i>fw</i> fore wing	<i>pl</i> prothoracic leg
<i>gt</i> developing genitalia	<i>pse</i> postclypeus
<i>hw</i> hind wing	<i>pt</i> prothorax
<i>l</i> labrum of larva	<i>st</i> thoracic sterna
<i>la</i> labium	<i>ts</i> tarsal segments
<i>lb</i> labrum of pupa	<i>I-III</i> thorax
	<i>1-10</i> abdominal segments

ANOMALA KANSANA - LIFE STAGES



INDEX

- Abundance, 58
- Aesalinae, 32
- Allorhina, 10
- Ammoecius, 44
- Amphicoma, 41
 - epipharynx, 25
- Anal orifice, 43
- Anomala, 44, 45, 63
 - abdominal segments, 41
- Anomala aenea*, 12, 48
 - clypeus and labrum, 21
 - epipharynx, 22
 - mandibles, 35
- Anomala binotata*, 13, 57
 - clypeus and labrum, 21
 - epipharynx, 28
 - life-cycle, 66
 - mandibles, 35
- Anomala innuba*, 9, 13, 63
 - epipharynx, 28
 - life-cycle, 67
- Anomala kansana*, 16, 45, 58
 - clypeus and labrum, 21
 - epipharynx, 28
 - life-cycle, 67
- Anomala ludoviciana*, 63
- Anomala orientalis*, 9
 - epipharynx, 28
- Anomala phyllopertha*, 28
- Anomalini
 - epipharynx, 28
 - life-cycle, 66
- Antennae, 18
- Aphodinae, 8
 - epipharynx, 24
 - oviposition, 48
- Aphodini, 24
- Aphodius, 20, 44
 - abdominal segments, 41
 - epipharynx, 24
 - food, 58
 - maxillae, 38
- Aphodius fimetarius*, 20, 24
- Aphodius porcus*, 71
- Aphodius rufipes*, 20
- Aphodius troglodytes*, 71
- Asiatic beetle, 9
- Ataenius inops*, 58
- Ateuchus, 44
- Bumble flower beetle, 9, 10
- Canthon, 17, 18, 22, 25
- Canthon ebenus*
 - clypeus and labrum, 20
 - mandibles, 34
 - maxillae, 38
- Canthon laevis*, 17, 18
 - clypeus, 20
 - epipharynx, 23, 25
 - hypopharynx, 39
 - labrum, 20
 - mandibles, 33, 34
 - maxillae, 37, 38
 - oviposition, 47
- Carrot beetle, 9
- Ceruchus picus*, 36
- Cetonia, 44
- Cetoniinae, 8, 70
 - epipharynx, 30
 - key to genera, 77
 - life-cycle, 70
 - maxillae, 38
 - oviposition, 47
 - spines, 41
- Chaetopisthes, 71
- Clypeus, 20
- Coprinae, 8
 - epipharynx, 23
 - mandibles, 35
 - maxillae, 37
 - stridulation, 45
- Coprini, 24
- Copris, 17, 71
- Copris carolina*, 20
- Copris lunaris*, 20
- Copris tullius (anaglypticus)*, 24
- Corythoderus, 71
- Coltapa, 29, 51
- Cotalpa lanigera*, 9, 13, 17, 45, 58
 - clypeus and labrum, 21
 - epipharynx, 29
 - hypopharynx, 39
 - life-cycle, 67
 - mandibles, 35
 - maxillae, 38
 - molting, 51
 - oviposition, 47
- Cotinis nitida*, 10, 58
 - epipharynx, 30
 - life-cycle, 70, 71
- Cremastochelius, 31
- Cremastochelius nitens*, 70
- Cyclocephala, 11, 61, 67, 69

- Cyclocephala immaculata*, 69
Cyclocephala villosa, 67
 Cyclocephalini, 29
- Development, 50
 Dichelonyx, 66
 Diplotaxis, 48, 66
 clypeus and labrum, 20
 epipharynx, 26
 mandible, 35
 Dor beetles, 8
 Dorcinae, 32
 Dorcus, 43, 44
 epipharynx, 32
 mandibles, 36
 Dung beetles, 8
 Dynastes, 48, 67
Dynastes tityrus, 30
 Dynastinae, 8
 epipharynx, 29
 key to genera, 76
 life-cycle, 67
 maxillae, 38
 oviposition, 47
Dyscinetus barbatus, 68
Dyscinetus trachypygus, 68
- Economic importance, 8
 Eggs, 47
 Epipharynx, 22
Euchlora frischii, 21
Euethola rugiceps, 68
 Euparia, 71
 Euphoria, 14, 18, 41, 64
Euphoria fulgida, 10, 13
 life-cycle, 70
Euphoria inda, 9, 17, 45
 clypeus and labrum, 21
 food, 58
 hypopharynx, 39
 life-cycle, 70
 mandibles, 36
 maxillae, 38
Euphoria sepulchralis, 10, 13
 clypeus and labrum, 21
 food, 58
 life-cycle, 70
- Fig-eater, 10
 Food habits, 54
 Friedenreichi, 71
- Geotrupes, 71
 epipharynx, 22
 striculation, 45
Geotrupes stercorarius, 25
 Geotrupinae, 8
 epipharynx, 25
 Glaphyrinae, 25
 Goldsmith beetle, 9
Gopherus polyphemus, 71
 Green June beetle, 10
 Gymnetini, 30
 Gymnopleuri, 71
- Habitat preferences, 55
 Hatching, 48
Heliocopris dominus, 47
 Hibernation, 61
 Historical review, 10
 Hypopharynx, 39
- Japanese beetle, 9, 42
 June-bugs, 8
- Keys, 73-81
- Labium, 40
 Labrum, 20
 Lachnosterna, 11, 44, 69
 Lamellicornia, 8
 Laparosticti, 8
 life-cycle, 71
 Legs, 42
Ligyrodes rclictus, 9
 clypeus and labrum, 21
 epipharynx, 30
 food, 58
 life-cycle, 68
 mandibles, 35
 method of rearing, 14
 oviposition, 47
 Ligyus, 21, 68
Ligyus gibbosus, 9, 17, 45, 57, 61
 clypeus and labrum, 21
 epipharynx, 30
 hypopharynx, 39
 life-cycle, 67, 68
 mandibles, 35
 maxillae, 38
 oviposition, 48
Ligyus tumulosus, 68
 Listochelus, 44
 Literature, 11, 12

- Lucanidae, 8
 abdominal segments, 41
 antennal segments, 19
 economic importance, 8
 epipharynx, 32
 hypopharynx, 40
 importance of family, 8
 key to genera, 77
 maxillae, 37
 number of species, 8
 oviposition, 47
 setation, 41
 sexual differences, 8
 stridulation, 45
 Lucanus, 10
 mandibles, 36
- Macroductylini, epipharynx, 28
 Macroductylus, 44
Macroductylus subspinosus
 epipharynx, 28
 life-cycle, 66
- Materials, 13
 May beetles, 8
 Maxillae, 37
 Melolontha, 44
Melolontha melolontha, 8
 life-cycle, 64
Melolontha vulgaris, 21
 Melolonthinae, 8
 epipharynx, 26
 key to genera, 75
 life-cycle, 64
 mandibles, 35
 maxillae, 38
 oviposition, 47
 spiracles, 43
 stridulation, 45
- Methods, 13
 Molting, 50
- Ochrosidia, 11, 61, 68, 69
Ochrosidia immaculata, 57, 61, 63
 clypeus and labrum, 21
 epipharynx, 27, 30
 life-cycle, 67, 68, 69
 mandibles, 36
- Onthophagus, 17, 22, 24, 71
Onthophagus pennsylvanicus, 20
 mandibles, 34
 maxillae, 38
- Oryctes, 44
Oryctes nasicornis, 70
Oryctes rhinoceros, 46
 Osmoderma, 10, 44
 epipharynx, 30
Osmoderma eremicola, 70, 71
 Oviposition, 47
- Parastasia, 44
 Passalidae, 8
 antennae, 19
 economic importance, 8
 epipharynx, 33
 hypopharynx, 39
 legs, 40
 maxillae, 37
 oviposition, 47
 setation, 41
 stridulation, 45
 thoracic annulets, 40
- Passalus, 16, 18, 41, 42, 43, 44
Passalus cornutus, 16
 antennal segments, 19
 clypeus and labrum, 22
 epipharynx, 33
 food, 8
 mandibles, 36
 stridulation, 46
- Pelidnota punctata*, 9, 13, 44, 58, 64
 epipharynx, 29
 life-cycle, 67
 method of rearing, 14
 oviposition, 47
- Phyllopertha, 44
Phyllopertha horticola, 12, 48
 epipharynx, 22
- Phyllophaga, 9, 11, 13, 15, 21, 23, 28, 33, 44,
 45, 47, 51, 56, 58, 59, 60, 61, 63
 abundance, 59
 food, 56
 hibernation, 61
 key to species, 78
 life-cycle, 66
 molting, 51
 oviposition, 47
 pupation, 63
 stridulation, 46
- Phyllophaga affabilis*, 51
 life-cycle, 65, 66
Phyllophaga anxia, 66
Phyllophaga arcuata, 12
 life-cycle, 65

- Phyllophaga bipartita*, 51
 life-cycle, 65
Phyllophaga burmeisteri, 65
Phyllophaga congrua, 60
 life-cycle, 65
Phyllophaga corrossa, 52
Phyllophaga crassissima, 13, 17, 45, 56, 59, 60
 clypeus and labrum, 21
 hypopharynx, 39
 life-cycle, 65
 mandibles, 34, 35
 maxillae, 38
Phyllophaga crenulata, 65
Phyllophaga cribrorsa, 27
Phyllophaga drakii, 66
Phyllophaga ephilids, 65
Phyllophaga fervida, 12
 life-cycle, 64
Phyllophaga fraterna, 65
Phyllophaga fusca, 64, 65
Phyllophaga futilis, 13
 epipharynx, 23, 26
 life-cycle, 65
Phyllophaga grandis, 65
Phyllophaga hirticula, 65
Phyllophaga ilicis, 65
Phyllophaga implicata, 13, 56
 life-cycle, 65
Phyllophaga inversa, 65
Phyllophaga lanceolata, 9, 56, 60, 62
 clypeus and labrum, 20
 epipharynx, 27
 life-cycle, 12, 65
 mandibles, 35
Phyllophaga longitarsa, 57
 life-cycle, 65, 66
Phyllophaga nitida, 66
Phyllophaga praetermissa, 52, 57
Phyllophaga rubiginosa, 13, 56, 59, 60
Phyllophaga rugosa, 13, 56, 59, 60
 life-cycle, 65, 66
Phyllophaga submucida, 13, 57, 60
 life-cycle, 65
Phyllophaga tristis, 57
 epipharynx, 28
 life-cycle, 12, 64, 65
Phyllophaga vandinei, 65
Phyllophaga vehemens, 13, 51, 60
 life-cycle, 64, 65
Phytalis, 44
Phytalis smithi, 64
Pinotus, 17, 40, 43
Pinotus carolina
 labrum, 20
 oviposition, 47
 thoracic annulets, 40
Pleocoma, 19
Pleurosticti, 8
Polyphylla, 44, 66
 epipharynx, 28
Polyphylla hammondi, 58
Polymoechus brevipes, 58
 clypeus and labrum, 21
 epipharynx, 29
 mandibles, 35
Popillia japonica, 9, 11, 43
 epipharynx, 22, 28
 life-cycle, 66
Psammobius, 71
 Pupation, 63

Radula, 41
Rhizotrogus, 44
Rhizotrogus fallenii, 21
Rhyssenus, 71
Rutelinae, 8
 epipharynx, 28
 key to genera, 75
 life-cycle, 66
 mandibles, 35
 maxillae, 38
 oviposition, 47
Rutelini
 epipharynx, 29
 life-cycle, 66

 Sacred beetle, 10
Scarabaeidae, 8
 abdominal segments, 41
 abundance, 60
 antennal segments, 19
 economic importance, 8
 egg stage, 48
 food, 54, 57
 hypopharynx, 39
 key to subfamilies, 74
 maxillae, 37
 striculation, 45
Scarabaeoidea, 8
 key to families, 73
Scarabaeus, 10, 71
Scarabaeus sacre, 10
 Segmentation, 40

- Serica, 44, 48, 66
 - epipharynx, 26
- Serica brunnea*, 21
- Setation, 41
- Sinodendron, 18, 43, 44
 - epipharynx, 32
 - mandibles, 36
- Sinodendron rugosum*
 - clypeus, 22
 - epipharynx, 32
 - mandibles, 36
- Spiracles, 43
- Spotted grapeleaf beetle, 9
- Stag-beetles, 8
- Stephanucha pilipennis*
 - clypeus and labrum, 21
 - epipharynx, 31
- Strategus, 18, 48, 67
- Strategus antaeus*, 70
 - epipharynx, 30
 - nest-building habits, 70
- Strategus mormon*, 47
- Strategus quadrifovatus*, 13
 - life-cycle, 68, 69
- Strategus titanus*, 68
- Stridulation, 44
- Strigoderma arboricola*, 13
 - epipharynx, 28
 - life-cycle, 67
- Taxonomy, 72
- Termitodius, 71
- Trichiotinus, 10, 18
- Trichiotinus piger*, 58, 70
 - epipharynx, 31
- Trichius, 10
- Triodonta (Serica) aquila*, 26
- Trogidae, 8
 - antennal segments, 19
 - economic importance, 8
 - epipharynx, 31
 - hypopharynx, 39
 - maxillae, 37
 - oviposition, 47
 - striculation, 44
- Trox, 8, 18
 - clypeus and labrum, 21
 - epipharynx, 31
 - food, 8
 - importance, 8
 - mandibles, 36
 - peritreme, 43
 - propleuron, 40
- Xyloryctes, 17
- Xylotrypes, 44

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SAWFLIES OF THE SUB-FAMILY
DOLERINAE OF AMERICA
NORTH OF MEXICO

WITH SIX PLATES

BY
HERBERT H. ROSS

An elaboration of a thesis submitted in partial fulfillment of the requirements for the degree of Master of Science in Entomology in the Graduate School of the University of Illinois.

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TABLE OF CONTENTS

	PAGE
Introduction.....	7
Explanation of terms.....	8
Acknowledgments.....	11
Biology.....	13
Life history.....	14
Habitat relations.....	15
Seasonal occurrence.....	17
Phylogeny.....	20
Taxonomy and nomenclature.....	24
Subfamily Dolerinae.....	24
Genus <i>Dolerus</i>	24
Subgenus <i>Dolerus</i>	25
Key for the separation of the nearctic species.....	27
Unicolor Group.....	33
<i>neocollaris</i>	33
subsp. <i>narratus</i>	35
<i>unicolor</i>	35
<i>borealis</i>	38
<i>nativus</i>	38
<i>illini</i>	39
var. <i>rufilobus</i>	41
<i>tectus</i>	41
Sericeus Group.....	42
<i>sericeus sens. lat.</i>	43
<i>sericeus sens. st.</i>	44
subsp. <i>parasericeus</i>	45
subsp. <i>centralis</i>	46
subsp. <i>neosericeus</i>	47
Bicolor Group.....	48
<i>versa</i>	48
<i>piercei</i>	49
<i>clypealis</i>	50
var. <i>nigrilabris</i>	51
<i>nortoni</i>	51
var. <i>nigritella</i>	53
<i>collaris</i>	53
var. <i>erebus</i>	55
var. <i>maculicollis</i>	55
var. <i>icterus</i>	56
<i>neoagcistus</i>	56
<i>bicolor</i>	58
var. <i>lestiticus</i>	59
var. <i>nigrita</i>	59
<i>agcistus</i>	59
var. <i>moroa</i>	61
<i>distinctus</i>	61

ILL
v.12³
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moramus.....	62
idahoensis.....	63
interjectus.....	63
eurybis.....	65
abdominalis.....	66
Similis Group.....	67
elderi.....	67
var. auraneus.....	69
var. rubicanus.....	70
var. melanus.....	70
nasutus.....	71
apriloides.....	72
yukonensis.....	74
similis <i>sens. lat.</i>	75
similis <i>sens. st.</i>	77
var. novicius.....	78
var. nummarius.....	79
var. tibialis.....	80
var. conjectus.....	80
subsp. nordanus.....	80
subsp. fumatus.....	81
subsp. simulans.....	81
subsp. nescius.....	82
nicaeus.....	83
aprilis.....	84
var. nocivus.....	85
coloradensis.....	86
tejonensis.....	87
Neoaprilis Group.....	88
neoaprilis.....	88
subsp. konowi.....	90
Frisoni Group.....	91
frisoni.....	91
Subgenus Loderus.....	92
Key for the separation of the nearctic species.....	93
apricus.....	93
var. alticinctus.....	95
napaeus.....	95
albifrons.....	96
acidus.....	97
Bibliography.....	99
Plates.....	103
Index.....	115

INTRODUCTION

The North American sawflies of the subfamily *Dolerinae* have never attracted the attention of students interested in the structure of the genitalia, and consequently have never been studied in so thorough a manner as the Eurasian species. Two or three workers have made notable contributions to our knowledge of the group, but their treatises are incomplete and do not cover the additional material which has since accumulated in the subfamily. The pioneer work was done by Norton, who, in 1867, first revised the Nearctic species known to him. MacGillivray, in 1916, keyed the eastern species, but some of the characters which he chose as criteria, in particular the punctuation and sculpture of the head, the punctuation of the mesonotum, and the striation of the post-tergite ("scutellar appendage" of MacGillivray), are too variable to be relied upon when applied to a large series of specimens. His key, also, does not include the western species, and it contains one or two evident mistakes, so that it is not a faithful guide to the Nearctic *Dolerinae*.

The Eurasian species, on the other hand, have received a great deal of attention. Several European workers have made careful studies of the female genitalia of the group, so that the status of the Palearctic forms is quite clear. It is interesting to note in this connection that Hartig, as early as 1837, figured parts of the saws of two or three species with such accuracy as to show us today definitely with which species he was dealing. Cameron, in 1882, used the dentation of the ventral edge of the saw of the female to aid in separating the British species. In 1913, Enslin illustrated his key to the Palearctic *Dolerinae* with line drawings of the lower portion of the saw, the lancet. A year later Morice published a comprehensive series of photomicrographs of the entire saws of thirty-six Palearctic species. More recently (1926) Zelochovtsev gave a series of line drawings illustrating the different types of saws, and drew from them his idea of the relationships within the group.

In this paper the attempt is made to apply to the Nearctic species of the *Dolerinae* the same critical examination of the genitalia which has been accorded the Palearctic forms. The masking of several species under the same color and the assumption of several color combinations by the same species have given rise to many homonyms and synonyms. On account of the complexity which has thus arisen, it has seemed advisable to select neotypes for the species of which the types can not be found. This has been a difficult problem in many cases, but with regard to each one the course has been followed which will permit of retaining the largest number of

names already in the literature. In some cases the saws of the females are characteristic of the species, in others the sheath, but in others again neither of these are of use except for complexes within the group, and in these cases an aggregate of other characters has been used.

Besides giving a mere tabulation and description of the species, an effort has been made to show the natural groupings and relationships within the subfamily. The almost complete picture afforded by the saws is in most cases well substantiated by the external morphology and to quite an extent by the male genitalia. There are, however, several points in the phylogeny open to question, and it is readily conceivable that some of the ideas brought out in this paper will be changed by further studies, especially of the immature forms.

In order to avoid confusion with the great color variations exhibited by some species, and to express the phylogenetic relations of closely allied forms, it has been necessary to use varietal and subspecific categories. In this paper, the term *variety* is used for forms differing from the typical condition of the species in color only and showing little or no geographic isolation; *subspecies* is used for forms differing from the typical form either in structure or markedly in color and geographic distribution.

In pursuing this revision, material has been assembled from all the major collections in North America, and from as many of the smaller ones as possible. Several thousands of specimens have been examined from a great many parts of the country, so that the distribution given for the various species should have some significance. The types of all but a few of the species have been studied and the genitalia removed from the majority of the types and examined. The types of the species to which I did not have access have very kindly been studied for me by other persons. A few types are no longer in existence.

Where so many specimens of a species have been examined and such a multitude of distribution records assembled that it is impractical to publish them all, the distributional data have been greatly condensed, but not in a way to obscure the general picture of the range of the species. Where, however, only scattered records have been obtained, they have been given in detail.

EXPLANATION OF TERMS

The terms used in this paper for the ridges, furrows, and areas of the head distinct to the sawfly group are chiefly those defined by MacGillivray (1916). For convenience, the definitions of those most frequently met are repeated here.

The *vertical furrows* (Figure 62, *f*) are the furrows situated on the dorsal aspect of the head, extending from near the lateral ocelli to the posterior margin of the head. They may be distinct and trench-like, reduced in length and pit-like, or reduced to linear scars.

The *postocellar area* (*po*) is the area on the dorsal aspect of the head directly behind the ocelli, bounded laterally by the vertical furrows. It may be rugose, pitted, or shining, and flat or mound-like.

The *postocular area* (*pc*) is the area on the dorsal aspect of the head lateral to the vertical furrows and posterior to the eyes, and includes the upper portion of the postgenae. Some authors have called this area the vertex, but since the postocellar area is also part of the vertex proper it does not seem advisable to use vertex in the restricted sense of the postocular area. In this paper the term *vertex* is used to designate the area comprising the entire dorsal portion of the head posterior to the eyes and ocelli.

The *ocellar basin* (*oc*) is the depression in front of the anterior ocellus. This area is rarely represented in the Dolerinae, but when present is usually shining and longitudinally striate.

The *malar space* is the area between the base of the eye and the base of the mandible.

For the thorax the current terms are used. The mesonotum (Figure 63) is divided into four lobes, the anterior lobe (*al*), consisting of two halves, two *lateral lobes* (*ll*), and a posterior lobe, the *scutellum* (*sc*). The posterior margin of the scutellum is differentiated into a crescentic or triangular area (*px*) for which the term *post-tergite* is used, after Smulyan (1923).

The *pectus* is the large flat area of the mesosternum below the mesoepisternum. In most species, in addition to the regularly scattered punctures, the pectus has a *diagonal row* of closely set punctures, two to four in width, extending from the postero-lateral corner to the antero-mesal corner.

The genitalia of the females play such an important part in the classification of this group that all the parts are named again in this paper to avoid confusion. The posteriorly-exserted, scabbard-like structure (Figure 1, *sh*) is called the *sheath* (Morice, 1912). MacGillivray's term "saw-guides" was a misnomer, since the lance (*sens* Rohwer) is the actual guide of the saw. The sheath consists of two similar chitinized plates, which form a housing for the saw. The saw (*ln* and *lt*) is composed of two similar blades closely applied together *in situ*. Each blade is made up of a dorsal half, the *lance* (*ln*), and a ventral half, the *lancet* (*lt*) (Rohwer, 1922). The lance is unarmed, firmly fixed at its base, capable of only a pendular movement, and the two are fused along the dorsal margin at the base. The lancet is attached to muscles within the abdomen and is moved in a saw-like backward and forward motion, slotted into the lance, which acts as a guide. Morice (1912) has shown that the "saw" is not used, strictly speaking, as a saw, but rather as a probing and macerating tool, the point being used first to produce a hole, which is then widened by a probing and sawing motion and lengthened into a linear, bleeding slit. To correct the erroneous use of the term "saw," Morice proposed the name *scalpellum* for this organ.

The Dolerinae exhibit a great diversity in lancet armature and it has been necessary to give names to the spines and processes which comprise it. The examination of a series of saws makes clear the origin and development of the different spurs and spines, and readily demonstrates their homology, so that one system of nomenclature applies equally well to both simple and complex forms. A hypothetical saw to illustrate all types of armature is shown in Figure 2. The lance is divided into segments by *annuli* (*b*), which are usually distinct. The segments at the apex are often rounded or angled dorsally, giving the lance a serrate or scalloped appearance. The ventral edge of the lancet is divided into *lobes* (*lb*) which are more or less toothed. These correspond closely in position to the segments of the lance, although annuli are not always present in the lancet. On the lateral face of the lancet are two rows of armature: a dorsal row of thin wing-like structures, the *alae* (*a*), extending diagonally across the dorsal half or three-quarters of the lancet and at an angle to the surface, and a row of spurs, the *spurettes* (*sr*), between the alae and the ventral margin. Each ala is produced into a sharp *alar spur* (*ad*) on its ventro-proximal angle, and frequently bears a row of spines, the *alar spines* (*ac*), along the basal margin. Where the annulus is present it often bears a row of spines, the *ventral spines* (*x*), between the ala and the spurette. Both the alae and the spurettes apparently arise as outgrowths of the annuli.

The simpler saws lack armature on the lateral face and have only the ventral lobes, which are more or less strongly dentate, as in Figures 41, 42, 43, etc. The first lateral armature to appear is the series of spurettes, which originate as very small outgrowths of the annuli near the ventral margin (Figure 50). The alar spurs, which are the fore-runners of the alae themselves, next appear, arising near the middle of the annuli (Figure 49). In Figures 52, 53, and 54 the enlargement of the alar spur and the development of the ala may be easily followed. The annulus is frequently broken between the alae and the spurette in the higher forms, but some species retain it intact (Figure 3). The spurette is always most distinct at the distal end of the saw, but towards the base it tends to coalesce with the ventral margin and becomes obscured as a tooth of the ventral lobes. The alar and ventral spines become conspicuous only in the *similis* group (Figures 57 to 59) and in the subgenus *Loderus* (Figures 4 to 6). In these the saw is of a highly developed nature.

For the convenience of students of other countries who may wish to use these names, Latin equivalents are given for the new terms proposed for the parts of the saw, as follows: annuli = *annuli*; ala = *ala*; lobe = *lobus*; spurette = *spiculella*; alar spur = *alaspicula*; alar spines = *alaspinulae*; ventral spines = *ventrospinulae*.

In addition to this armature, the lancet possesses two other structures, a linear chitinated strip (Figure 2, *r*) running the length of the dorsal mar-

gin of the lancet and ending in its extreme tip, and a series of duct-like "fingers" (Figure 44) leading into the lobes. The function of the "rod" (*r*) is undoubtedly to assist in forming a runner with the lance, and to strengthen the lancet. The function of the duct-like structures is problematic, but they may very likely be ducts through which secretions are applied to the wound made in the tissues of the host plant at the time of the sawing of the egg cavity or the laying of the egg.

The only parts of the male genitalia which are mentioned in this paper are the sclerites of the ventral aspect (Figure 64) for which the names established by Crampton (1919) are used. The parapenis, or *praeputium* (*pp*), is composed of the two large sclerites which form the central plate of the capsule; the *gonocardo* (*g*) is the crescentic sclerite below the praeputium; and the *gonostipes* (*st*) are the lateral sclerites adjacent to the praeputium and bearing the claspers, or *harpes* (*h*), on their apical margin. Within the cylinder formed by the gonocardo and gonostipes is situated the penis, composed of two paired rod-like structures. The upper portions, between the harpes, are the penis valves (*v*), and the lower portions, projecting beneath the gonostipes, are the penis rods (*p*).

The same sclerites are represented throughout the entire subfamily, varying only in their proportions. As a rule the type of genital capsule is constant for the groups herein treated, but there are one or two exceptions. They lack specific characters, however, so that they are of little value in identification.

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BIOLOGY

But little is known of the life habits and immature stages of the North American Dolerinae, because most of the species frequent situations seldom studied by the entomologist, some are apparently rare, and none are of more than trivial economic importance.

The first records of the habits of these insects were the result of complaints from various sources that adults of *Dolerus unicolor* chewed the buds of pear trees, causing them to drop. Forbes (1885) investigated the matter and found that they "were neither biting nor piercing the buds or flowers, but that they were merely licking off the semi-fluid exudation from the surface of the bud scale." He added: "Dissecting the specimens and examining the contents of their stomachs with the microscope, I found only a clear fluid, without a trace of solid matter, except occasional spheres of clusters of threads of fungus parasites. . . . Watching the flies with a glass, I could see that their biting jaws remained all the time closed, but that their flap-like maxillae were continually employed in mopping up the moisture from the viscid surface." He observed two species of *Dolerus*, which his descriptions indicate were *D. unicolor* and *D. neoagcistus*. The first rearing work to be done was that of Riley and Marlatt (1891), who drew attention to the fact that the species of *Dolerus* are among the earliest sawflies to appear in the spring and are very commonly taken on grass, particularly in moist and swampy localities. They described several types of larvae feeding on grasses and bred adults of two species, *D. unicolor* and a specimen determined as *D. collaris*, neither being definitely associated with any one of their described types of larvae, but certainly from larvae feeding on timothy grass (*Phleum pratense* L.). The record for *D. collaris*, however, can not be accepted without verification, since there are several species of the same color which have all been identified as *collaris* by the older workers. The need for work on the immature stages was expressed by MacGillivray (1913) in the following summary: "None of the larvae of the Dolerinae have been absolutely identified for the North American forms. What are believed to be larvae of this subfamily are grass and sedge feeders. They usually occur singly or several individuals on the same stem, clasping it with their thoracic and abdominal legs." Yuasa (1922), in studying the group, reared *D. similis* from larvae on the common horsetail, *Equisetum arvense*, and definitely established the identity of that species. In addition, he described seven other unidentified larvae which fed on grasses, sedges, or horsetail. Yuasa's work is the most recent in the field.

The European workers are almost equally in the same plight in regard to the Palearctic species of *Dolerus*. Of these species, which total about forty, only six have their larvae definitely known, with an additional three or

four very doubtfully established (Enslin, 1913). Of these, *D. madidus* and *haematodes* feed upon *Juncus*, *D. nigratus*, *gonager*, and *pratensis* feed on grass, and *D. palustris* on *Equisetum*. Konow (1901) lists, in addition, *D. coruscans* and *D. gibbosus* as doubtfully feeding on grasses, and keys this group of eight species by means of color pattern.

During the course of an intensive collecting campaign in the spring of 1929, several habitats were discovered which appeared to be ideal for the development of several species of *Dolerus*. The three most interesting places were situated at Seymour, Savoy, and Ogden, all within fifteen miles of Urbana, Illinois, where this work was undertaken. Of these, the Seymour area was most frequently visited, about fifteen collecting trips being made there between April 14 and June 14, 1929. From 50 to 500 specimens of *Dolerus* were collected on each trip. The data, although far from final or conclusive, being the result of only one year's observations, nevertheless bring out somewhat forcefully two conclusions: first, that the different species of the genus appear in a definite seasonal succession; and, second, that certain species are very definitely associated with certain ecological conditions and are useful as indicators of certain habitats. These results would be rendered more indicative if the immature stages were associated for certain with the adults, but for the present the probable identification of the larvae, based upon circumstantial evidence, is of great assistance. It is the author's intention to continue these observations over a number of years, and to make every attempt to rear the larvae of all the species on these areas; but, meanwhile, since our knowledge of the biology of the genus *Dolerus* is so scant, it seems worth while to present now this introduction to a study of the subject.

LIFE HISTORY

All the species of *Dolerus* which have been observed in Illinois appear to have the same life-cycle, the type common to many groups of sawflies. In spring the insect emerges as an adult from the hibernation quarters in the ground. The males appear in large numbers before more than a few females have appeared, the latter becoming proportionately more numerous as the season advances, until towards the latter part of the regime of the species the females far outnumber the males. Little mating is apparent except on warm sunny days, when both sexes fly about very actively and are often seen in copulation. The eggs are laid in the tissues of the host plant, deposited in a cavity specially formed by the "saw," or scalpellum, of the female. This process was described in great detail by Morice in 1914. The young larvae, soon after hatching from the egg, become external feeders upon their host. Those feeding upon sedges or grasses clasp the lateral edges of the blade and eat portions out of the sides. The young larvae of those feeding upon *Equisetum* also eat out lateral portions of the

terete siliceous needles, but the larger larvae climb to the top of a needle and chew it completely down in one gradual operation. In about a month the larvae become full-grown and enter the ground, where they pass the late summer, fall, and winter. In Illinois three species feeding on *Equisetum*, namely, *D. similis*, *D. aprilis*, and *D. apricus*, dig among the roots of thick clumps of horsetail in fairly dry, well-drained soil to a depth of three or four inches, where they form an earthen cell. No cocoon is spun, either for a hibernaculum or for a pupal case. An *Equisetum*-feeding species occurring in British Columbia performed the same operations in preparation for hibernation. In early spring the larvae transform to pupae, and shortly thereafter into adults, which dig out of the ground and assume the activities of reproduction.

The Illinois species have only one generation each year, as is well shown by the fact that subsequent collecting in their favorite habitats never reveals more than a rare, stray specimen after the first wave of abundance of the species. The data borne by pinned specimens of the other species of the genus point to the same conclusion, so that the entire genus may be said to be characterized by a one-year cycle.

The larvae are entirely phytophagous, their hosts being chiefly various species of grasses, *Carex*, *Equisetum*, and *Eleocharis*, and possibly other species of the sedge and rush families. The food of the adults seems to consist entirely of sweet secretions of plants, such as nectar of flowers and flowing sap of trees. Adults of *D. unicolor* and *D. neoagcistus* are taken in great numbers feeding on the nectar of flowers of *Crataegus*, *Prunus*, etc., or on the sap of the sugar maples. *D. similis* and *D. aprilis* are frequently taken on the flowers of willows which occur near their breeding places. It is not likely that they partake of much solid food, for the proventriculus, or gizzard, has not a strong grinding apparatus.

HABITAT RELATIONS

A detailed study of the habitat relations of the commoner species of *Dolerus* was made possible through the unique position of the habitats most frequented by these species. Running east, north, south, and west from Urbana are railway lines, paralleled by concrete highways, with a multitude of habitats, ranging from the wettest swamps to the driest of prairie situations, along the railway embankments. In certain of these areas the sawflies were found to be very abundant, and it was quite easy to go by automobile on the highways along these railroad lines and collect at a great many places of diverse ecological conditions and to determine exactly which were preferred by each species. It is remarkable that while sawflies of this genus abounded at many points along these lines of habitats, practically none were present on the vast extent of farm lands stretching on either side. Unless the railroad sites were chosen for a collecting venture,

a worker might conclude that these sawflies were of rare occurrence in this part of the state—a conclusion erroneous in the extreme, yet doubtless explaining why so many collections lack an abundance of some of the more habitat-selective species found during our excursions of 1929.

The habitat relations of the species which have been observed in detail appear to be constant and precise. Not only was each species definitely associated with the occurrence of its one host, but many were limited to local areas possessing very definite degrees of ecological conditions, indicated by the combination of plants growing thereon.

Here might be noted some of the habits of the adults which rendered their collection easy. In early spring when the first common species began to appear as adults, the ground was barren except for the stripped stalks of the weeds which had grown there the previous year, such as *Solidago*, *Silphium*, etc., and the bare stems of the willows. Upon these the adult sawflies preferred to rest; and upon cold, wet days, with which April abounded, they clung in great numbers to these slender posts, became inactive and almost torpid with the cold, and could be picked off with the fingers very quickly and efficiently. They clung so tightly that the picking process proved much faster than sweeping with the net. On warm, sunny days it was necessary to sweep, for they became too active to catch with the fingers. Later in the season sweeping *Equisetum* produced large numbers of *D. similis* and *D. apricus*.

The types of habitat in which *Dolerus* was studied are as follows:

1. Sedge (*Carex*), horsetail (*Equisetum arvense*), and willow (*Salix*) communities. Low, semi-swampy areas.
2. Horsetail and grass communities. Dry, well-drained areas, where a firm, long-undisturbed sod was developed.
3. Grass communities. Wet prairie situations with a preponderance of the coarser grasses rather than the finer grasses of cultivation.

An ideal example of the first type of habitat, sedge-horsetail-willow, was found at Seymour (Figure 72). Between a railroad embankment on one side and a state highway on the other was an area about twenty-five feet wide, swampy in the wetter seasons of the year and with a few inches of standing water in the rainy period of early spring. The plant population consisted chiefly of a mixture of a single species of *Carex* that was fairly luxuriant when in full growth, the common horsetail, and a scattering of the stalks of a small willow, most of which were dead. The species characteristic of this habitat and found in no other were *D. illini* and *D. agcistus*, which are *Carex*-feeding forms. *D. aprilis* and *D. similis*, which feed on *Equisetum*, were also abundant here but were taken plentifully elsewhere.

The extreme selectivity of *D. agcistus* and *D. illini* was demonstrated by collections made along the railroad in many localities north of Urbana. Collections were made every few miles along this stretch, but a represen-

tation of these two species was taken only from those areas which seemed identical with the Seymour habitat in all particulars, even to the presence of a few dead willow twigs. Spots which supported a luxuriant growth of the same species of *Carex* as the ideal type of habitat, but which were drier, had at most a very few specimens of *Dolerus*.

The horsetail-grass type of habitat was exemplified by areas along the railroad at Savoy (Figure 73), situated four miles south of Urbana; at Ogden, fifteen miles east of Urbana; and also at Seymour. In these places the two apparent essentials for the prolific development of *Dolerus* were an old, well-formed sod and a dry, well-drained soil. At Savoy only *D. aprilis* and *D. similis* were present, but in very great numbers. On one occasion about 200 specimens were taken in 100 linear yards of sweeping. At Ogden and Seymour, in addition to these two species, *D. apricus* was very abundant. In these latter two places, also, a small brown larva was found feeding on *Equisetum* late in July, after all the others had disappeared. It is suspected that this is the larva of *D. apricus*. Of the three species found in these *Equisetum* habitats, *D. similis* was least selective in its habitat preferences, for it was found in almost every kind of situation wherever there was a growth of *Equisetum*. *D. aprilis* was perhaps no more selective, but may have been missed in later collections at some points because its height of abundance was earlier. *D. apricus*, on the other hand, was very selective, being found only in areas in which the horsetail, grasses, and weeds appeared to be long established.

The coarse grass habitats were studied very little in this survey, for after investigations were well under way little remained in these situations but larvae. In the spring of 1928, however, it was noticed that *D. unicolor* appeared there very early in the spring in large numbers; and subsequent sweeping unearthed a large, abundant, cream-colored *Dolerus* larva believed to belong to this species. In captivity these larvae fed readily on any of the species of grass found in this habitat. Collected with them and feeding on the same grasses were *Dolerus* larvae which were white with lateral black spots (*Dolerus* sp. 2 Yuasa, 1922). It is possible that these larvae may be *D. neoagcistus*, which is an early species, and often taken at flowers with *D. unicolor*.

Although no evidence of the fact had been noticed in 1929 collecting, there may be also a distinct forest-inhabiting group of *Dolerus*, for *D. nortonii* has been taken in the vicinity of Urbana in original forested land only, especially in University Woods, which is a semi-swampy woodland and may harbor certain sedges or grasses fed upon by the larvae of this species.

SEASONAL OCCURRENCE

In this region the various species of *Dolerus* are among the very first of the hibernating insects to become active at the onset of spring. The

first individuals usually appear during the last two weeks of March, and by mid-April their numbers are manifold. By late June, however, most of the adults have disappeared, and by late July the larvae also have disappeared, so that the active period of the group as a whole is short. In regions where they occur abundantly, these sawflies are undoubtedly the first group of insects to be important defoliators of the vegetation, and they must hold a high place in the economy of such areas. This is further supported by the fact that in 1929, until midsummer, the specimens of *Dolerus* far outnumbered other species of insects taken on *Equisetum* and *Carex*; and the larvae seemed to attract a great number of parasitic Hymenoptera belonging to groups which are known to parasitize sawflies.

Data on the seasonal occurrence and abundance of the adults of the species of *Dolerus* taken in all localities during the season of 1929 are shown in Table I, and a summary of the data for the Seymour area alone is shown in Figure 71.

TABLE I—TOTAL NUMBER OF SPECIMENS OF *DOLERUS* COLLECTED
AT ALL LOCALITIES IN ILLINOIS DURING 1929

	March		April				May				June				July	
	15- 22	23- 31	1- 7	8- 15	16- 23	24- 30	1- 7	8- 15	16- 23	24- 31	1- 7	8- 15	16- 23	24- 30	1- 7	8- 15
<i>D. unicolor</i>		1	66	2		9										
<i>D. neoagcistus</i>			4			3										
<i>D. illini</i>				139	20	15										
<i>D. collaris</i>			1													
<i>D. aprilis</i>			1	191	70	13	134	51		2						
<i>D. neoaprilis</i>				3	1		4									
<i>D. agcistus</i>				53	4	73										
<i>D. apricus</i>							2			155		70	4			
<i>D. similis</i>				13	23	124	59	8	9	71	11	19	61		12	

D. neoaprilis, *D. collaris*, and *D. neoagcistus* were represented by so few specimens that they may be passed over as of merely incidental interest, and as possibly being rarities in this region. Urbana is likely the extreme southern limit of distribution for the first two, but all three of these species may prove to be abundant with further exploitation. *D. unicolor* is the first species to make its appearance. In 1928 and 1929 the adults were flying during the last week in March, and in 1930 they were extremely abundant on March 15. In 1929 they reached their peak of abundance during the first week of April, and thereafter soon dwindled away.

The next species to occur in large numbers were *D. illini*, *D. aprilis*, and *D. agcistus*. On April 14 these species were all at their greatest abundance at Seymour; but it is doubtful if they occur as early as *D. unicolor*. It is very probable that the great proportion of the population of each species of this group emerges within a comparatively short time, so that the graphic curve of their rise in numbers would be very steep, as is that

of *D. apricus*. *D. illini* and *D. aprilis* were especially abundant, while *D. agcistus* was only moderately plentiful. *D. agcistus* and *D. illini* disappeared from the area very rapidly.

In the Seymour region this wave of species had receded by about the first of May, except for a few specimens of *D. aprilis*, and left the field to *D. similis*. This latter species never reached very great numbers in the Seymour habitat but was represented in moderate quantities for about two months—a much greater length of time than any other species. This could be explained by various reasons: (1) greater longevity, (2) a natural tendency for different individuals to take a different length of time to develop, or (3) the selection of different hibernation sites by the larvae, so that they are subject to different temperatures in the early developmental period of spring, hence to different rates of growth, and as a result would emerge as adults over a longer period of time. It will be remembered from the discussion of habitat relations that *D. similis* is also the only species observed which was not apparently restricted to a certain type of habitat, but occurred abundantly wherever its food plant was plentiful, which strongly suggests the last alternative to account for its long period of adult activity. This species was much more abundant at Savoy and Ogden than at Seymour, and it is probably the most common species in the state, or at least second in rank to *D. unicolor*.

The last species to appear on the scene was *D. apricus*. At the Seymour habitat it appeared quite suddenly on the 21st. of May, and its numbers rose in a few days to their highest point. About three weeks after its first occurrence it was rapidly on the decline, and after the middle of June it together with *D. similis* formed the final retreat of the adults of *Dolerus* for the season.

PHYLOGENY

The phylogeny of the Dolerinae is based essentially upon the picture of the development of the saw from the simple to the complex. It may be argued that such a utilitarian attribute should be disregarded in a consideration of phylogeny, since it is apt to vary within natural groups without respect to relationships, due to differences in the host plants of species within the same group. In this case, however, the grouping afforded by the saws is readily upheld by external morphological characters and to quite an extent by the male genitalia, which seems to me quite significant in a group so lacking in conspicuous specific characters. Also, from the meager evidence which can be collected, host selection seems to be a link in the phylogenetic chain. While other characters alone present good criteria for super-specific grouping, they do not show so clearly as the saws that which is so necessary to a family tree, namely, direction of development.

Zhelochovtsev (1926), using the evidence furnished by the Palearctic forms, considered the development within the subfamily to be linear, but when the Holarctic fauna is considered, there appear distinct groups which follow a line of development at divergence with the others. The point of origin of the different groups is speculative, of course, but the developmental lines within the groups are distinct.

The *unicolor* group is regarded as the most primitive outgrowth of the Dolerinae stem. In the lowest members, e.g., *D. neocollaris*, the postocular area is very large and the eyes are therefore comparatively small. The saw is many-segmented, the lancet lacks lateral armature, and the annuli are represented by oblique areas of minute spines. The lobes are distinct and only very minutely toothed. In the higher forms the postocular area becomes slightly shorter and the lobes more coarsely toothed. The *sericeus* group probably branched off from the main stem near the same place as did the *unicolor* group. In saw characters these two groups are very similar, but morphologically the *sericeus* group is quite distinct from all other members of the subfamily, except *D. frisoni* Ross, in having the hind tibiae very clearly grooved on both the inner and outer sides, and, in the male, in having a triangular procidentia on the caudo-mesal portion of the eighth tergite. *D. frisoni* is a puzzling case which is discussed under the treatment of the species. The conformation of the pleurae and pectus of the *sericeus* group is also characteristic. The lancet in this group is simple, lacking lateral armature except in *D. neosericeus*, where rudimentary alae are developed. The lobes are distinct and coarsely dentate, and annuli are usually well indicated. A subgeneric name could be applied to this group with good

justification, for it is certainly as definitely separated from the mass of the Dolerinae as is the subgenus *Loderus*, but since it appears as only one group among the many in the general perspective of the subfamily it seems unwise to split the genus further.

It would appear that a dichotomous split occurs in the family tree above the point from which sprang the lower groups, one branch giving rise to the *bicolor* group and the other giving rise to the *similis* group and its allies. In the *bicolor* group the various steps in the development of the lateral armature of the saw are very graphically illustrated. In *D. collaris* (Figure 50) the annuli are distinct, with a small spurette developed at the ventral margin. In *D. clypealis* (Figure 49) first indications of alae appear near the dorsal margin of the lancet, the spurettes still being rudimentary. Progressing through *D. neoagcistus*, *D. bicolor*, and *D. agcistus*, the development of the alae and spurettes can be followed with clarity. In this group the alar and ventral spines are not developed. From the opposite stem arose the *similis* and *neoaprilis* groups, and the subgenus *Loderus*. The first two probably branched off close together, as the saw characters would indicate. The *similis* group exhibits a progressive reduction of the teeth of the lobes, a marked coalescence of the spurettes with the lobes, and a development of both alar and ventral spines. In the *neoaprilis* group the spurettes are distinct, the lobes have many fine teeth, the Palearctic species *D. dubius* has both alar and ventral spines, and the Nearctic species *D. neoaprilis* has only ventral spines. *Loderus*, which is characterized by long, emarginate eyes, seems to present a group of saws of a highly developed nature, but on analysis the difference between the saws of *Loderus* and the *similis* group is not as great as that between those of the *similis* and *unicolor* groups. The saw of *L. apricus* suggests a close relationship with the *elderi* section of the *similis* group. The chief differences are that in *L. apricus* (Figure 5) the alar spurs have become separated from the alae, and the spurettes are entirely fused with the ventral lobes. The other species of *Loderus* contain two types of saws (Figures 4 and 6) which are markedly different from each other and show no clear relationship to other groups in the subfamily. It seems apparent, however, that they have arisen from the series possessing alar spines; and the long, emarginate eyes, the development of alar spines, and (in *L. albifrons*) the coalescence of the spurettes with the ventral lobes, suggest their position as among the most highly developed group in the subfamily.

From the evidence furnished by the saws, *Loderus* is at most a highly specialized group comparable to other groups within the Dolerinae, and follows a chain of development from the lowest forms in the subfamily. *Loderus* Konow is therefore considered in this paper as being of only sub-generic rank. This viewpoint is further supported by a consideration of the character upon which *Loderus* is differentiated from *Dolerus*, namely,

the condition of the eyes. In the *unicolor* group, particularly *D. neocollaris*, the eyes are short and the postocular area long; in the *similis* group the eyes are longer and the postocular area short, while in some species the inner margin of the eyes show a distinct tendency to be emarginate; in *L. acidus* and *L. albifrons* the eyes are no longer than in *D. similis* but are distinctly emarginate; and in *L. apricus* the eyes are very long and emarginate. At no point in this gradation can a line be drawn to separate the subfamily into two distinct units.

The distribution of the subfamily is amazingly uniform. It is exclusively Holarctic, occurring in Northern Africa, throughout the Eurasian region with the exception of India and the Malayan region, and throughout North America. It is of especial interest, however, to note that almost all the groups into which the subfamily may be divided are represented throughout the Holarctic region. The greater number of the Nearctic species of *Dolerus*, and all the Nearctic species of *Loderus* have identical structural homologues in the Palearctic region. It is evident, therefore, that the group *Loderus* has not developed in geographic isolation, but with the rest of the *Dolerinae*.

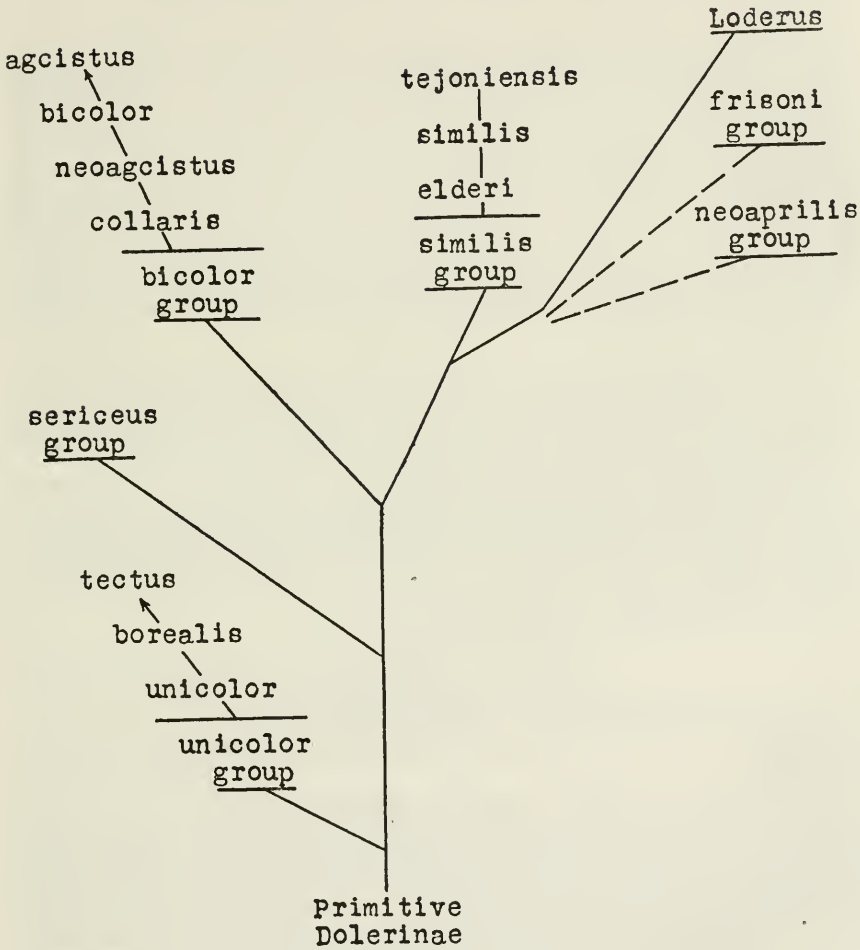
It is interesting in this connection to note that complexity of saw structure has progressed hand in hand with host selection. The evidence on this point is meagre, since very few of the larvae of this group have been reared, but what there is of it points out a fairly clear path. The following tabulation summarizes the host relations which have been found in the literature:

TABLE II

Group	Species	Host
Unicolor	<i>D. unicolor</i>	<i>Phleum pratense</i>
	<i>D. nigratus</i>	<i>Festuca</i> sp.
	<i>D. gonagra</i>	<i>Festuca</i> sp.
Unicolor?	<i>D. madidus</i>	<i>Juncus</i>
	<i>D. haematodes</i>	<i>Juncus</i> and <i>Scirpus</i>
Bicolor	<i>D. collaris</i>	Rushes (<i>Eleocharis</i> ?)
Similis	<i>D. pratensis</i>	<i>Equisetum arvense</i>
	<i>D. palustris</i>	<i>Equisetum arvense</i>
	<i>D. similis</i>	<i>Equisetum arvense</i>
	<i>D. nicaeus?</i>	<i>Equisetum arvense</i>

The species with the simple saws choose for hosts the soft-tissued grasses, the species with highly developed, complex saws have hosts of a hard, siliceous texture. It will be interesting to find the host relationships of the higher members of the *bicolor* group, of the *neoaprilis* group, and of the subgenus *Loderus*.

The following diagram gives the author's conception of the phylogenetic tree of the subfamily:



TAXONOMY AND NOMENCLATURE

SUBFAMILY *DOLERINAE*

- Dolerides* Thomson, Hymen. Scandin., Tom. I, 1871, p. 278.
Dolerides Cameron, Monog. Brit. Phyt. Hymen., Vol. I, 1882, p. 157.
Dolerinae Dalla Torre, Cat. Hymen., Vol. I, 1894, p. 1.
Dolerinae Ashmead, Can. Ent., Vol. XXX, No. 12, Dec., 1898, p. 306.
Dolerides Konow, Gen. Insectorum, Hymen., Fam. Tenth., 1905, p. 68.
Dolerinae MacGillivray, Proc. U. S. Nat. Mus., Vol. XXIX, 1906, p. 628 and p. 631.
Dolerinae Rohwer, Proc. Ent. Soc. Wash., Vol. XIII, 1911, p. 221, and p. 222.
Dolerini Enslin, Tenth. Mitteleur., Deutch Ent. Zeits., 1912, Beiheft, p. 40.
Dolerinae MacGillivray, Bull. No. 22, Conn. Geol. Nat. Hist. Survey, 1916, p. 68.

Members of this subfamily are characterized by the venation of the front wings (Figure 70), in particular the contraction of the anal cell and the presence of only two closed submarginal cells, due to the loss of the middle transverse cubital vein, or R_5 of MacGillivray. The group is a compact one, with a distinct habitus. The body is stout, short in comparison to its width as compared with other groups, such as the Tenthredininae and Allantinae. The clypeus is slightly asymmetrical, the sinistral lobe being slightly smaller than the dextral. The greater area of the head and thorax is opaque and punctate, usually clad with whitish pile, which is especially conspicuous on the lower portion of the head.

Existing determinations in the group have been found so unreliable that only records that have been seen by the author are considered valid. Particularly misleading errors in the literature have been commented upon to bring them into conformity with the records in this paper.

In the subfamily and generic bibliography many references have been omitted which dealt only with exotic groups, and in the bibliography of each species references to faunal or local lists have been omitted. The subfamily consists of only the one genus, *Dolerus*, which is therefore defined by the characteristics of the subfamily.

GENUS *DOLERUS* Jurine

Litt.-Zeitung Erlanger, Vol. I, Nro. 21, May 30, 1801, p. 163.

Genotype.—*Dolerus gonagra* Fabricius (Subsequent designation of Latrielle, 1810).

The date of the original description of the name *Dolerus*, in common with many other Hymenopterous generic names, is tied up with the "Erlangen List" of Panzer, published in the daily scientific journal of Erlangen, and forgotten by entomologists until it was again brought to light by the work of Morice and Durrant (1915). These two authors have shown that the name *Dolerus*, accompanied by two constituent species, *D. germanica* and *D. gonagra*, was first published in this work. Rohwer (Ent. News, 1911) accredits the genus to Panzer and gives the place of original description as "Fauna Insectorum Germaniae," Heft 82, Jahrgang 7. Morice and Dur-

rant (loc. cit.), however, state that this latter Volume bears the date "September 3, 1910," whereas the Erlangen List was published on May 30 of the same year. Latrielle (1810) set *D. gonager* Jur. as the type of *Dolerus*, and since this species was included under *Dolerus* in the original description, it is a valid designation. The type set by Rohwer in 1911, viz., *Dolerus pedestris* Panz. (= *D. pratensis* L.), would be valid only if the second reference were the place of the original description. The author is in accord with the arguments and opinions of Morice and Durrant in accrediting the name *Dolerus* to Jurine and not to Panzer.

The genotype represents a member of the *unicolor* group as represented in this paper, which would therefore be considered as the genus in the very strictest sense should anyone elevate these groupings to subgeneric rank. Leach, in 1817, separated from *Dolerus* the genus *Dosytheus*, naming first in the latter *D. eglanteriae* Klug (= *D. pratensis* L.), which belongs to the *similis* group. These two genera have been considered synonymous by subsequent authors. A study of the Nearctic forms indicates clearly that these groups are worthy of only group names, and are not of generic or subgeneric rank. In 1890, Konow proposed the new genus *Loderus* for the species of *Dolerus* which had the inner margin of the eyes emarginate, but for reasons given in the treatment of phylogeny, *Loderus* is considered as a subgenus.

KEY FOR THE SEPARATION OF THE SUBGENERA

1. Eyes emarginate on their mesal margin; malar space shorter than the length of the first antennal segment (Figure 16); tarsal claws toothless or with a small tooth (Figures 11 and 12).....LODERUS KONOW
- Eyes almost straight on their mesal margin, short, the malar space usually as long as the length of the first antennal segment (Figure 15); tarsal claws always toothed (Figures 13 and 14).....DOLERUS JURINE

SUBGENUS *Dolerus* Jurine

Dolerus Jurine, in Panzer, Litt. Zeitung Erlanger, Vol. I, Nro. 21, May 30, 1801, p. 163.

Dolerus Panzer, Fauna Insect. German., VII, p. 82, T. 11, 1801.

Dolerus Panzer, Krit. Revis., Vol. 2, 1806, p. 40.

Dolerus Jurine, Nouv. Meth. Class. Hymen., 1807, p. 57; T. 2 F. 4.

Dosytheus Leach, Zool. Misc., Vol. III, 1817, pp. 127-128.

Dolerus Leach, *ibid.*

Dolerus Lepeletier, Monograph. Tenthred., 1823, p. 116.

Dolerus Cresson, Jour. Bost. Soc. Nat. Hist., Aug., 1861, p. 37.

Dosytheus Norton, Proc. Bost. Soc. Nat. Hist., Vol. VIII, 1862, p. 151.

Dolerus Norton, *ibid.*, p. 154.

Dolerus Norton, Trans. Amer. Ent. Soc., Vol. I, 1867, p. 231.

Dolerus, Sectio II, Thomson, Hymen. Scandin., Tom. I, 1871, p. 278 and p. 281.

Dolerus Cresson, Trans. Amer. Ent. Soc., Vol. VIII, Feb., 1880, p. 58.

Dolerus Cameron, Monog. Brit. Phyt. Hymen., Vol. I, 1882, p. 157.

Dolerus Provancher, Faun. Entom. Can., Hymen., 1883, p. 195.

Dolerus Cresson, Trans. Amer. Ent. Soc., Supp. Vol. for 1887, p. 15, p. 161.

Dolerus Dalla Torre, Cat. Hymen., Vol. I., 1894, p. 1.

nec Dolerus Guillebeau, Ann. Soc. Ent. France, Vol. LVIII, 1894, p. 282 and p. 307. (Phalacridae, Coleop.).

Dolerus Ashmead, Can. Ent., Vol. XXX, No. 12, Dec., 1898, p. 306.

Dolerus Konow, Genera Insectorum, Hymen., Fam. Tenth., 1905, p. 110.

Dolerus MacGillivray, Bull. No. 22, Conn. Geol. Nat. Hist. Survey, 1916, p. 69.

Distinctive characters of the subgenus those given in the key. Eyes straight on their mesal margin and short in length; malar space variable, usually as long as the first antennal segment; clypeus coarsely punctate, sub-truncately cleft, the dextral lobe usually slightly longer than the sinistral; the area above the cleft transversely carinate; tarsal claws bearing a tooth which may be either small, as in Figure 15, or large and coarse as in Figure 14; antennae and punctuation of head and thorax variable; pleurae more or less coarsely punctate, pectus in comparison smooth and finely punctate; sheath well clad with setae, both sheath and saw extremely variable.

Genotype.—*Dolerus gonagra* Fabricius (Latrielle, 1810).

This subgenus lacks an abundance of good specific characters, and hence the species are often difficult to separate. In the *bicolor* group it is essential to base determinations on an examination of the saw. In the *similis* and *sericeus* groups the saw is of little value for separating closely allied forms, and an aggregate of other characters must be used. The differences in these two latter groups are largely relative, so that a worker has to familiarize himself with the group to make close and accurate comparisons. The males of many species can be readily separated, but there are some groups in which no characters have yet been found to distinguish between the species, even when the males are known and at hand. The genitalia are very helpful in separating out the groups, but do not show differences beyond that. It is therefore necessary, although regrettable, to key some species only to the group.

KEY FOR THE SEPARATION OF THE NEARCTIC SPECIES

1. Females (abdomen with an apical sheath-like structure, Figure 1).....2
- Males (abdomen with a flat and entire apical sternite, Figure 7).....46
2. Hind tibiae deeply, longitudinally grooved on both inner and outer sides; large black species, with post-tergite smooth and shining.....*sericeus* Say
- Hind tibiae distinctly grooved only on inner side if at all, sometimes very slightly on outer side, except occasionally *apriloides*, which has the abdomen rufous; color and post-tergite various.....3
3. Head, pleurae, pectus and abdomen metallic blue in color, collar and mesonotum mostly yellow; sheath as in Figure 22, with the ventrocaudal margin emarginate, with a tuft of hairs at the apex.....*unicolor* (Beauv.)
- Body, except sometimes head, not metallic blue, but black or black and rufous; sheath various.....4
4. Sheath long, emarginate on the ventro-caudal margin, the extreme apical portion with a distinct scopa; setae short, tufted at apex, giving the sheath a horned appearance (Figure 22); postocular area twice as long as eye, seen from above; size large, body black except sometimes part of thorax.....5
- Sheath various (not as in Figure 22), either short or without a tuft of setae at extreme tip; postocular area often long, but not twice length of eye.....6
5. Body entirely black.....*neocollaris* subsp. *narratus* MacG.
- Anterior lobe rufous.....*neocollaris* MacG.
6. Abdomen and most of thorax black, at most with indistinct fuscous area on disc, sides, or base of abdomen.....7
- Abdomen mostly rufous, at least with two terga rufous or a distinct rufous area on dorsum of abdomen, in the latter case the metapleurae often being in part rufous....19
7. Lateral lobes rufous, anterior lobe black.....*borealis* MacG.
- Lateral lobes either the same color or darker than anterior lobe.....8
8. Postocular area long, flat and robust; sheath thin and blade-like; post-tergite smooth and shining, without a median carina; large species, at least 8.5 mm. in length....9
- Not with the above combination of characters; either with the postocular area narrowed behind eyes, or the sheath thick and short, or the post-tergite carinate and more or less sharply striate.....10
9. Body entirely black; sheath angled on ventral margin (Figure 17).....*tectus* MacG.
- Usually with pronotum and anterior lobe rufous, sometimes with the lateral lobes also rufous, sometimes almost entirely black except for clouded rufous areas on the anterior lobe and pronotum; sheath rounded on ventral margin, not angled (Figure 23)....*illini* Ross
10. Sheath with a distinct scopa along the distal margin (Figures 28, 30, 31 and 32), with a number of setae near the middle of the distal margin much longer than the rest, pleurae usually finely, and always evenly, punctate, never depressed above the pectus; pectus often shagreened.....11
- Sheath without a scopa (Figures 33 to 40), the setae in an evenly graduated series; pleurae usually coarsely and unevenly punctate, often depressed above the pectus; pectus shining except sometimes in *neoaprilis*.....16
11. Scopa narrow or indistinct, at most as wide as in Figure 28; saw without alae, sometimes with small, peg-like lateral teeth (Figures 49 and 50).....12
- Scopa wider (Figures 30 to 32), rim of scopa often rounded; saws with lateral teeth and well developed alae (Figures 52 to 54).....14

12. Scopa indistinct, sheath long, as in Figure 26, cerci attaining only half length of sheath; saw as in Figure 51, the basal tooth of the lobes projecting as a finger-like process *nortoni* var. *nigrella* Ross
- Scopa distinct, sheath shorter and wider (Figure 27); saw as in Figure 50, without the basal tooth of the lobes conspicuous 13
13. Body entirely black except sometimes for an indistinct rufous spot on collar *collaris* var. *erebus* Ross
- Collar and usually anterior lobe rufous *collaris* Say
14. Saw with very wide lateral teeth (Figure 54); sheath thick and wide; body entirely black *idahoensis* Ross
- Saw narrow, without very wide lateral teeth (Figure 53); sheath thick, but narrower than in *idahoensis* 15
15. Body entirely black, except sometimes for an indistinct rufous mark on collar *bicolor* var. *nigrita* Ross
- Collar and anterior lobe rufous, sometimes upper pleurae and part of lateral lobes rufous *bicolor* var. *lesticus* MacG.
16. Sheath armed with short, stiff, black and bristle-like setae; upper and lower margins of sheath convex, sheath thick at base, pointed at apex (Figure 36) *neoaprilis* subsp. *konowi* MacG.
- Sheath armed with longer, finer, usually silky setae; upper margin straight, tip of sheath not bi-convexly pointed 17
17. Postocular area rotund (Figure 7), evenly punctate, with at most a very shallow furrow before the posterior margin; size small, less than 8 mm. *elderi* var. *melanus* Ross
- Postocular area usually narrowed behind eye, either with a deep transverse furrow before posterior margin or densely and coarsely punctate; size larger, 8 mm. or more. . . 18
18. Sheath wide, lateral carina diverging from dorsal margin towards apex (Figure 34), and distant from it; head black from all angles; postocular area rarely shining, usually opaque; saw as in Figure 59 *nicaeus* MacG.
- Sheath narrow, lateral carina approximate to and converging with, dorsal margin, meeting it at tip (Figure 35); inner orbits giving a bluish reflection in some positions; anterior part of postocular area shining, the punctures distinct from each other; saw as in Figure 57 *nasutus* MacG.
19. Vertex and dorsum of thorax without punctures, or at most with one or two minute impressions; abdomen entirely rufous *tejonensis* Nort.
- At least postocellar area and lateral margins of anterior lobe bearing several punctures. 20
20. Punctures on thorax very few, and indistinct; lateral areas of anterior lobe with only a few small punctures; postocular area impunctate, shining; size large, 11 mm.; abdomen entirely rufous. *coloradensis* Cress.
- Punctures on thorax quite distinct, sides of anterior lobe densely punctured; postocular area punctate, although often shining; size and color variable 21
21. Metapleurae and adjacent sutures of mesopleurae entirely or partly rufous; mesopleurae evenly punctate, often finely so; sheath with a number of setae on ventral margin much longer than the others; abdomen usually rufous, sometimes with venter black and part of dorsum also, but never with first four or five segments rufous and apex black 22
- Metapleurae and adjacent sutures black; mesopleurae usually roughly punctate, often indented just above pectus, with a number of larger punctures in the depressed portion; sheath, except in *D. interjectus*, with setae in a more or less evenly graduated series, not with a few very long ones on the ventral margin; abdomen sometimes entirely rufous, often with the first four or five segments rufous and the apex black. . . 35
22. Anterior lobe black, lateral lobes rufous 23

- Anterior lobe either same color as lateral lobes, or rufous and the lateral lobes black . . . 24
- 23. Anterior lobe very finely and evenly punctate, dull *piercei* Roh.
- Anterior lobe shining, lateral punctures large and distinct, sparse posteriorly . . . *versa* Nort.
- 24. Wings checkered; apical portion hyaline, basal portion deeply purplish brown infusate *eurybis* Ross
- Wings almost uniformly hyaline or infusate 25
- 25. Thorax entirely black (paraptera sometimes rufous), abdomen entirely rufous 26
- Thorax in part rufous 27
- 26. Sclerites forming base of sheath black; pleurae with fairly small punctures *agcistus* var. *maroa* Ross
- Sclerites forming base of sheath rufous; pleurae with fairly large punctures *abdominalis* (Nort.)
- 27. Venter of abdomen mostly black, dorsum rufous 28
- Abdomen entirely rufous, sometimes with small areas washed with black 29
- 28. Sheath very wide, scopa wide, angled laterally (Figure 32); saw as in Figure 54; size large, 10 mm.; Pacific Coast species *distinctus* Nort.
- Sheath smaller, scopa narrower; size smaller, not exceeding 8.5 mm.; saw as in Figure 50 *collaris* var. *maculicollis* (Nort.)
- 29. Clypeus rufous; sheath triangular, scopa very narrow; saw as in Figure 49 . . . *clypealis* Ross
- Clypeus black 30
- 30. Cerci not more than one-half dorsal length of sheath, sheath long (Figure 26); scopa lacking or very indistinct; saw with basal angle of lobes produced in a finger-like projection (Figure 51); small species, length 6 mm. *nortoni* Ross
- Cerci reaching almost to tip of sheath, sheath short or angular at apex; with a distinct, though sometimes narrow, scopa; ventral margin of saw not as in Figure 51 31
- 31. Saw with only rudimentary alae (Figures 49 and 50); scopa narrow, no wider than in Figure 27 32
- Saw with alae distinct (Figures 52 to 54); scopa wider (Figures 30 to 32) 34
- 32. Saw sub-triangular, as in Figures 49 and 61; sheath angular at apex, ventral margin straight 33
- Saw ellipsoidal, as in Figure 50; sheath usually with ventral margin rounded *collaris* var. *icterus* MacG.
- 33. Spurettes and alar spurs of saw distinct and finger-like (Figure 61); wings dusky *piercei* Roh.
- Spurettes more or less distinct, alar spurs very rudimentary (Figure 49); wings hyaline *clypealis* var. *nigriabris* Ross
- 34. Scopa oblique (Figure 30), lateral margin angular; saw as in Figure 52; tarsal claws small *neoagcistus* MacG.
- Scopa more squarely and roundly truncate, if oblique, then lateral margins rounded; saw not as in Figure 52 35
- 35. Saw as in Figure 53; sheath small; tarsal claws with a small tooth; size small, 7 to 8.5 mm. *bicolor* (Beauv.)
- Saw as in Figure 54; sheath larger (Figure 32); some of tarsal claws with a large, coarse tooth (Figure 13); size larger, 8.5 to 10 mm. 36
- 36. Wings only slightly brownish infusate *agcistus* MacG.
- Wings deep chocolate infusate at base, shading to lighter at apex *moramus* Ross
- 37. Sheath truncate, with a wide scopa, with a few setae on the caudal margin much longer than the others (Figure 31); postocular area without distinct furrows; saw as in Figure 54 *interjectus* Ross
- Sheath without a scopa, with the setae in an evenly graduated series (Figures 33 to 40), without some setae on the ventral margin longer than the others; saw not as in Figure 54 38

38. Small species, 6 mm. in length; dorsum of thorax black; if slightly larger, then postocular area rotund, laterally expanded (Figure 7), without deep furrows, polished and sparsely punctate. 39
- Larger, at least 8 mm. in length, or with anterior or lateral lobes rufous; postocular area either deeply transversely furrowed, or densely punctate, sometimes with a transverse shining ridge. 39
39. Femora rufous, entirely or in great part. *elderi* var. *rubicanus* Ross
- Femora black, except sometimes their apices. 40
40. Abdomen entirely rufous, at most with a portion of the last two segments black; wings slightly infusate. *elderi* var. *auraneus* Ross
- Abdomen with three or four apical segments black; wings usually hyaline. *elderi* Kinc.
41. Sheath clothed with short, dense, black, bristle-like setae; sheath thick at base, tapering towards apex, the latter pointed (Figure 36); clypeus very deeply notched; pleurae with some very large punctures in a conspicuously depressed area over pectus *neoaprilis* MacG.
- Sheath clothed with slender setae, not thick and bristle-like; sheath not as in Figure 36 42
42. Sheath long and rhomboidal, as in Figure 39, the black chitinized portion longer than wide. 43
- Sheath shorter and less truncate than in Figure 39, the black chitinized portion as wide as long. 44
43. Thorax black. *aprilis* (Nort.)
- Thorax in part rufous. *aprilis* var. *nocivus* MacG.
44. Meso-episternum very deeply rugose, the rugosities extending to the very edge of the pectus; meso-episternum depressed above the pectus, the edges of the depression obscured by the large pits; division between pleurae and pectus sudden and ridge-like; sheath as in Figure 35, with a distinct dorso-lateral corner; saw as in Figure 57 *apriloides* MacG.
- Meso-episternum sometimes coarsely, but never deeply punctate, and never so rugose. 45
45. Ventral portion of apical red tergites black, the black decreasing towards the base of the abdomen, forming a tapering black margin on the venter from apex to base; pleurae fairly smoothly punctate, merging into the pectus, the division not sharply defined; saw as in Figure 57. *yukonensis* Nort.
- Red tergal plates entirely red, not black on venter; pleurae more or less coarsely punctate, the division between pleurae and pectus distinct and ridge-like; saw as in Figure 59 *similis* (Nort.)
46. Body mostly metallic blue in color. *unicolor* (Beauv.)
- Body not metallic blue, except sometimes head; color black, or black and rufous 47
47. Abdomen entirely rufous. 48
- Abdomen in part black. 52
48. Vertex impunctate, polished, shining; dorsum of thorax and pectus shining, impunctate; dorsum of thorax rufous except sometimes anterior lobe. *tejonensis* Nort.
- Vertex, dorsum of thorax and pectus punctate, at least lateral areas of anterior lobe with distinct punctures. 49
49. Mesonotum entirely black. 50
- Mesonotum in part rufous. 51
50. Wings deeply chocolate-infusate basally, clear at apex. *eurybis* Ross
- Wings uniformly hyaline. *abdominalis* (Nort.)
51. Anterior lobe black, lateral lobes rufous. *versa* Nort.
- Anterior lobe rufous, lateral lobes black. *moramus* Ross
52. Abdomen entirely black. 53

- . Abdomen with at least two, usually with four to six, terga rufous.....63
- 53. Eighth tergite with a median, subtriangular, apical projection or procidentia; legs distinctly grooved on both inner and outer sides; body entirely black.....*sericeus* Say
- . Eighth tergite without a procidentia, although sometimes carinate on the meson; legs not grooved on outer side, rarely on inner; if grooved, then abdomen mostly rufous...54
- 54. Postocular area twice as long as eye, seen from dorsal aspect, latero-caudal corner much rounded.....53
- . Postocular area less than twice as long as eye, usually shorter or subequal in length; if nearly twice as long, then quadrate or robust on the corners.....56
- 55. Occurring in the Rocky Mountains and westward; pleurae usually with abnormally long pubescence.....*neocollaris* subsp. *narratus* MacG.
- . Occurring east of the Rocky Mountains; pubescence of pleurae of the usual length.....*neocollaris* MacG.
- 56. Anterior lobe rufous.....*illini* var. *rufilobus* Ross
- . Anterior lobe black.....57
- 57. Posterior margin of post-tergite round; surface highly polished and shining, without a median carina.....58
- . Posterior margin of post-tergite pointed; surface at least faintly striate, with a more or less distinct carina.....59
- 58. Posterior angle of anterior lobe with distinct, large punctures.....*tectus* MacG.
- . Posterior angle of anterior lobe smooth and striate, impunctate.....*illini* Ross
- 59. Clypeus deeply notched, at least halfway to base; post-tergite usually shining, striae granular and rounded; pleurae sharply indented above pectus, indented portion with large irregular punctures.....*neopapilis* subsp. *konowi* MacG.
- . Clypeus notched only one third way to base; post-tergite usually distinctly striate, striae sharp; pleurae little if at all indented above pectus.....60
- 60. Pleurae evenly, more or less "velvety" punctate, punctures small, walls of punctures low, not sharp; sides of anterior lobe with distinct dot-like punctures; third to fifth abdominal sternites three to four times wider than long.....*nortoni* Ross
collaris Say
neoagcistus MacG.
bicolor (Beauv.)
agcistus MacG.
- . Pleurae with large crater-like punctures, walls of punctures sharp and high; sides of anterior lobe with uneven, rugose punctures; third to fifth abdominal sternites only twice as wide as long.....59
- 61. Size small, 7 mm. or less; postocular area robust and round, evenly, sparsely punctate, without ridges.....*elderi* var. *melanus* Ross
- . Size larger, 8 mm. or more; postocular area narrowed behind eyes, transversely ridged, unevenly or densely and coarsely punctate.....62
- 62. Head with an area lateral of ocelli with a bluish reflection; postocular area with a central shining area, only sparsely punctate.....*nasutus* MacG.
- . Head without an area with a bluish reflection; postocular area entirely opaque with punctures.....*nicaeus* MacG.
- 63. Postocular area impunctate, polished; mesonotum and pectus practically impunctate, polished; lateral portions of anterior lobe shining, with only faint, sub-obsolete punctures.....*coloradensis* Cress.
- . Postocular area with distinct, often dense, punctures; lateral portions of anterior lobe dull or rough, densely or coarsely punctured.....64
- 64. Pleurae finely punctured, punctures very small and equal, not crater-like with sharp walls.....65

- Pleurae more coarsely punctured, punctures large and crater-like, with sharp, distinct walls; punctures around margin of meso-episternum smaller, those in centre larger. . . . 66
65. Wings hyaline, except for a slight tawny staining near base; size small, 7 mm.
..... *interjectus* Ross
- Wings infusate on basal half; size larger, 8.5 mm. *nativus* MacG.
66. Size small, 6 mm.; postocular area robust and shining, sparsely punctate without a transverse ridge midway between eye and posterior margin of head; pleurae with large, round punctures, very distinct, shallow and saucer-like. 67
- Size larger, 7 mm. or more; postocular area either densely punctate, or with a distinct transverse ridge; punctures of pleurae, if large, with sharp walls, crater-like. 69
67. Femora rufous, except sometimes basal third. *elderi* var. *rubicanus* Ross
- Femora mostly black. 68
68. Wings clear hyaline. *elderi* Kinc.
- Wings slightly infusate; occurring in the southern Rocky Mountains
..... *elderi* var. *auraneus* Ross
69. Eighth tergite with a carinate procidentia extending the entire length of the segment, gradually ascending to a point at apex; meso-episternum depressed above pectus, with large rugosities in the depression. *frisoni* Ross
- Eighth tergite without a procidentia, sometimes slightly carinate on the meson. 70
70. Meso-episternum rugosely punctate, depressed above pectus, the wall of the depression high and sharp or obscured by large rugosities; the third and fourth antennal segments subequal; hypopygium long. 71
- Meso-episternum not so coarsely punctate, at most feebly depressed above pectus; clypeus about one-third cleft; third antennal segment longer than fourth; hypopygium short, the corners often sharp. 72
71. Walls of depression of pleurae high and sharp, not obscured by rugosities; punctures of pleurae shallower; hypopygium more rounded at apex. *neoaprilis* MacG.
- Walls of depression of pleurae obscured by rugosities, more or less indefinite; punctures of pleurae deeper; hypopygium squarely truncate at apex. *apriloides* MacG.
72. Ventral portion of apical red tergites in part black, the black decreasing towards the base, giving a striped appearance to the venter; pleurae and pectus merging imperceptibly, making an even, smooth bevel. *yukonensis* Nort.
- Red tergal plates red on venter also, or if black with the base of the wings fairly deeply infusate; division between pleurae and pectus well defined, usually ridge-like
..... *similis* (Nort.)
..... *aprilis* (Nort.)

UNICOLOR GROUP

Females.—Postocular area, except in *borealis*, usually long; clypeus notched only one-third its length; antennae fairly stout, third segment slightly longer than fourth, the remainder very gradually diminishing in length; pleurae smoothly and evenly punctate, sometimes with a few larger punctures near centre; hind tibiae not grooved on outer side, slightly grooved on inner; tarsal claws with a small, erect tooth; sheath long, blade-like, in some species with a narrow scopa at tip; cerci attaining only half dorsal length of sheath; saw simple, without lateral teeth.

Males.—Similar to females, except *unicolor*, which has a shorter postocular area; genitalia as in Figure 65; praeputium long, angular at base, apices rounded and only slightly diverging; gonocardo very narrow; pedes wide and truncate.

Dolerus neocollaris MacGillivray

Dolerus neocollaris MacGillivray, Can. Ent., Vol. XL, No. 4, April, 1908, p. 127; MacGillivray, Bull. 22, Conn. Geol. Nat. Hist. Surv., 1916, p. 71; Frison, Bull. Ill. Nat. Hist. Surv., Vol. XVI, Art. IV, Feb., 1927, p. 242.

Dolerus refugus MacGillivray, Can. Ent., Vol. XL, No. 4, April, 1908, p. 127; MacGillivray, Bull. 22, Conn. Geol. Nat. Hist. Surv., 16, p. 71; Frison, Bull. Ill. Nat. Hist. Surv., Vol. XVI, Art. IV, Feb., 1927, p. 244. *New synonymy*.

Female.—Length 8.5 to 10 mm. Body almost entirely black except collar, anterior lobe, most of pleurae above pectus, and minute ring at apex of femora, rufous. Tibiae sometimes slightly lighter than body. Wings hyaline.

Postocular area very long, seen from above twice as long as eye, the postero-lateral corners round; posterior margin of head very much sinuate; vertical furrows wide and trench-like, reaching posterior margin; postocellar area longer than wide, raised and distinct from postocular area; lateral ocelli closer to each other than to posterior margin of head; head entirely reticulately punctate, the punctures sparser and more distinct just behind eye; posterior margin of postocular area with a slight but distinct ridge, the furrow in front of it very densely punctate. Centre of anterior lobe very finely punctate, shining, lateral areas rough, coarsely punctate; lateral lobes closely punctate with minute pits; post-tergite triangular, smooth and shining, sometimes obscurely striate, subcarinate, slightly depressed transversely, the posterior margin angular, the extreme point smooth and rounded; pleurae evenly and finely, yet roughly, punctate; pectus shining, with distinct, fairly large punctures. Sheath as in Figure 22, long, the ventral portion thin, gradually increasing in thickness dorsally, the apex terminating in a distinct apical scopa on which is a thick tuft of short setae,

giving the sheath a horned appearance; dorsal margin slightly concave, ventral margin slightly convex, more or less distinctly shouldered at the ventro-caudal angle, slightly emarginate just below the tip; cerci at most attaining half dorsal length of sheath; setae on both sheath and cerci short and silky, except on "horn" of sheath. Saw as in Figures 41 and 42; lance with about 28 annuli; apex serrate, base very large; lancet with about 23 lobes, the lobes distinct and extremely minutely dentate; annuli represented by linear areas of minute spines.

Male.—Length 8 to 9.5 mm. Color entirely black; wings hyaline. Structure very similar to female. Head usually narrower behind eyes than through them, entirely coarsely reticulately punctate; third segment of antennae shorter than fourth, fourth and fifth subequal, last four almost subequal, but slightly shorter towards apex, last segment three-fourths as long as third. Punctures on anterior lobe larger than in female; central portion shining, lateral portion rough, posterior third with sparser large punctures; lateral lobes shining, with very small punctures; pleurae very finely punctate; pectus shining and minutely punctured; post-tergite triangular, more or less sharply carinate along meson, usually obscurely striate and transversely depressed, the posterior margin angular. Ninth tergite one-third as long as eighth, caudal and mesal portions white; hypopygium long, the apical half trowel-shaped, the sides converging and the tip rounded; ventral aspect of genital capsule as in Figure 65.

Holotype.—♀, Fulton, New York, April 27 (C. R. Crosby). In the MacGillivray Collection, University of Illinois, Urbana, Ill.

Lectoallotype.—♂, Ithaca, New York, April 23, 1896. Deposited with holotype. (Frison, 1927).

Distribution.—A scarce species of which the following specimens have been examined: COLORADO: 1 ♀, Colo. (C. F. Baker). ILLINOIS: 1 ♂, Normal, Apr. 30, 1884; 2 ♀ ♀, Urbana, Apr. 30, 1892 (Marten); 3 ♀ ♀, Devil's Hole, Havana, Apr. 6, 1917; 1 ♂, Urbana, Mar. 27, 1928 (H. H. Ross); 2 ♂ ♂, 16 ♀ ♀, Savoy, April 9, 12 ♀ ♀, Champaign, April 10 and Gray Lake, April 23, 1930 (Frison and Ross). IOWA: 4 ♀ ♀, Ia.; 1 ♂, Mt. Pleasant, Apr. 11, 1928 (Purdy). MASSACHUSETTS: many specimens from Westfield, Amherst, Lexington, Salem and Tynsboro, April and May. MICHIGAN: 1 ♀, Detroit, Apr. 22, 1920 (S. Moore); 1 ♀, Ann Arbor, May 7, 1919 (T. H. Hubbell). MISSOURI: 1 ♀, Mo. (C. V. Riley). MONTANA: 1 ♂, 3 ♀ ♀, Bozeman, Apr. 26 to Jun. 26; 2 ♀ ♀, Gallatin Co., Apr. 25, 1926. NEBRASKA: 1 ♀, Roca, Apr. 13, 1918 (Brunner); 1 ♀, Lincoln, Apr. 23, 1916 (Dawson); 1 ♂, Neb. NEW YORK: many specimens from Richfield Springs, Ithaca, Syracuse, Onondaga County, Cayuga, Johnstown, Stephentown, and Albany, April, May, and August. OHIO: 1 ♀, Columbus, Apr. 9, 1925 (O. Cartwright); 1 ♀, Cedar Point, July 7, 1915 (V. R. Haber). SOUTH DAKOTA: 1 ♂, Brookings, May 20, 1914.

WISCONSIN: 1♂, Madison, Apr. 30, 1920 (Gentner). ONTARIO: ♂♂ and ♀♀, Ottawa, May to August; 1♀, Vineland, Apr. 24, 1927 (W. G. Garlick). QUEBEC: 1♀, Montreal, Apr. 29, 1900 (A. F. Winn); 1♀, Montreal, Jn. 3, 1906; 1♀, Montreal, May 7, 1927 (J. W. Buckle); 1♀, Aylmer, May 1, 1921 (C. B. Hutchings); 1♀, Isle de Montreal, May 20, 1906.

The female of this species is most easily confused with *illini*, from which it is readily distinguished by the sheath. The male can be recognized by the great length of the postocular area, and the pointed post-tergite. The female has often been mistaken for similarly colored species of the *bicolor* group, but can easily be separated from them on the basis of group characters and the sheath.

A series of this species from Montana contains a female with only the anterior lobe rufous, which is midway between the typical form and race *narratus*. A male specimen associated with this series has the long pubescence found in males associated with *narratus*.

Dolerus neocollaris subsp. *narratus* MacGillivray

Dolerus narratus MacGillivray, Can. Ent., Vol. LV, No. 3, Mar., 1923, p. 65; Frison, Bull. Ill. Nat. Hist. Surv., Vol. XVI, Art. IV, Feb., 1927, p. 242.

Dolerus nocuus MacGillivray, Ins. Insc. Mens., Vol. XL, Nos. 1-3, 1923, p. 34; Frison, Bull. Ill. Nat. Hist. Surv., Vol. XVI, Art. IV, Feb., 1927, p. 243. *New synonymy*.

Female.—Length 9 mm. Color entirely black.

Structure almost identical with *neocollaris*. Differs only in having the antennae more slender, and the anterior portion of the lateral lobes almost impunctate. Genitalia as in *neocollaris*.

Male.—Length 8 mm. Color entirely black.

Can not be readily separated from typical *neocollaris*. In some specimens the pubescence on the head and thorax is very much longer than in the typical form, but this is a common adaptation to higher altitudes.

Holotype.—♀, Mary's Peak, Corvallis, Oregon, May 14 (A. L. Lovett). Deposited in the MacGillivray Collection, University of Illinois, Urbana, Ill.

Lectoallotype.—♂, Mary's Peak, Corvallis, Oregon, May 23 (Zwicker). Deposited with the holotype. (Frison, 1927).

Distribution.—IDAHO: 3♀♀, Moscow. OREGON: 1♂, 2♀♀, Mary's Peak, Corvallis; 1♂, Entermille; 1♂, 2♀♀, Corvallis. WASHINGTON: 3♂♂, 2♀♀, Pullman, Apr. 3 to 25. BRITISH COLUMBIA: 1♂, Vernon, Apr. 25, 1919 (N. W. Ruhmann); 1♀, Vernon, Apr. 6, 1915 (M. H. Ruhmann); 1♀, Glacier; 1♂, Victoria, Apr. 12, 1917 (A. E. Cameron).

Dolerus unicolor (Beauvois)

Tenthredo unicolor Beauvois, Insect. Afr. and Amer., 1805, Hymen., p. 97, ♂.

Tenthredo thoracinus Beauvois, *ibid.*, ♀.

Dolerus thoracinus Lepeletier, Monog. Tenthred., 1823, p. 122; Dalla Torre, Cat. Hymen., Vol. I, 1894, p. 10.

Dolerus thoracicus Kirby, List Hymen. Brit. Mus., Vol. I, 1882, p. 230.

Dolerus unicolor Lepeletier, Monog. Tenthred., 1823, p. 122; Norton, Proc. Boston Soc. Nat. Hist., Vol. VIII, 1861, p. 152; Norton, Trans. Amer. Ent. Soc., Vol. I, 1867, p. 234; Provancher, Nat. Canad., Vol. X, 1878, p. 70; Riley, Amer. Nat., Vol. XV, 1881, p. 574; Provancher, Faun. Entom. Can., Hymen., 1883, p. 196; Gillette, Ent. News, Vol. I, 1890, p. 94; Dalla Torre, Cat. Hymen., Vol. I, 1894, p. 10; MacGillivray, Can. Ent., Vol. XL, No. 4, April, 1908, p. 130; MacGillivray, Bull. 22, Conn. Geol. Nat. Hist. Surv., 1916, p. 73.

Dolerus arvensis Say, Keatings Narrat. Exped. II, 1824, App., p. 319; Leconte, Writ. Thomas Say on Entom., Vol. II, 1859, p. 214; Norton, Proc. Boston Soc. Nat. Hist., Vol. VIII, 1861, p. 152; Norton, Trans. Amer. Ent. Soc., Vol. I, 1867, p. 234; Provancher, Nat. Canad., Vol. X, 1878, p. 70; Thomas, 10th. Rep. State Ent. Ill., 1880, 1881, p. 67; Provancher, Faun. Entom. Can., Hymen., 1883, p. 196; Forbes, 14th Rep. St. Ent. Ill. f. 1884, 1885, p. 100; Packard, Rep. U. S. Ent. Comm., Vol. V, 1890, p. 587; Riley and Marlatt, Insect Life, Vol. IV, 1891, p. 171.

Male.—Length 8 to 9 mm. Body metallic blue, except mouthparts, labrum, clypeus, eyes, antennae, dorsum of meso- and metathorax except sides of anterior lobe, tegulae, pectus, legs, and genital capsule, which are black; wings almost hyaline, veins black.

Head uniformly reticulate; eyes prominent; postocular area very slightly longer than eye, seen from above, narrowed behind eye, almost flat, but with a moderately small, sharp transverse ridge, posterior margin raised and ridge-like; vertical furrows deep and trench-like, separated from posterior margin by a narrow partition; postocellar area also reticulate, flat, slightly raised above level of postocular area; antennae bilaterally compressed, third and fourth segments subequal, the remainder gradually and almost imperceptibly decreasing in length. Mesonotum, except sides of anterior lobe and most of post-tergite, shining, sparsely and more or less minutely punctate; sides of anterior lobe reticulate, like head and pleurae; post-tergite shining, usually shagreened, which gives a sparkling reflection, subtriangular, slightly to moderately transversely convex, without a median ridge; meso-episternum finely, smoothly and evenly reticulate; pectus very smooth and shining, slightly shagreened, fairly densely punctured, diagonal row visible but somewhat indistinct; tarsal claws sharply curved, with a small tooth. Eighth tergite with a very fine median carina for its entire length; hypopygium long and convex; sides of apex slightly concave, apex arcuately rounded. Genitalia as for group.

Female.—Length 9 to 10 mm. Body mostly metallic blue, with the following parts yellowish-rufous: prothorax, sides of anterior lobe and lateral lobes; with the following parts black: mouthparts, clypeus, antennae, middle of anterior lobe, scutum, post-tergite, metanotum, pectus, legs, ninth and tenth tergites and sheath. This is the color phase described and figured by Beauvois for *Tenthredo* (*Dolerus*) *thoracinus* (1805). Most specimens encountered have the anterior half of the lateral lobes black, while a

few have the mesonotum entirely black with the exception of several small rufous spots in the corners of the lobes. Wings brownish infusate, slightly darker than in the male.

Body very robust. Head uniformly reticulate except sometimes postocellar area and transverse ridge of postocular area which may be more sparsely punctate and shining; postocular area distinctly longer than eye, seen from above, robust, not narrowed behind eye, with a low, wide, raised transverse area, posterior margin without a carina; vertical furrows very wide and trench-like, only two-thirds as long as postocellar area; postocellar area either flat and reticulate or convex, punctate and shining; third antennal segment slightly longer than fourth, fourth longer than fifth, remainder almost sub-equal. Mesonotum, except sides of lateral lobe and post-tergite, shining, sparsely punctured, but more heavily than in *neocollaris*; sides of anterior lobe evenly reticulate; post-tergite as in male, shagreened, dull shining, sub-triangular and convex, not carinate; meso-episternum, pectus and tarsal claws as in male; sheath and saw exactly as in *neocollaris*.

Neotype.—♂, Oakwood, Illinois, March 17, 1927, flying over grass where female was found (T. H. Frison). Deposited in the collection of the Illinois State Natural History Survey, Urbana, Ill.

Distribution.—An early, common and widely distributed species throughout the eastern and central United States and south-eastern Canada. Over two thousand specimens of this species, including about equal numbers of both sexes, have been examined from the following states: Colorado, Connecticut, Delaware, Georgia, Illinois, Indiana, Iowa, Kansas, Kentucky, Maine, Maryland, Massachusetts, Michigan, Minnesota, Missouri, District of Columbia, Nebraska, New Hampshire, New Jersey, New York, Ohio, Pennsylvania, South Dakota, Virginia, Wisconsin, Manitoba, Ontario and Quebec.

A large species, easily distinguished in both sexes by the brilliant metallic blue color of the greater part of the body. Alcoholic specimens lose the metallic coloration, in which case the female may be distinguished by the sheath and the pattern of the dorsum of the thorax, and the male by the very long antennae and the genitalia.

The amount of black on the mesonotum of the female varies considerably, from being a single mark on the anterior lobe to covering almost the entire area. The intermediate form is most frequently taken in collections. Apparently none of the color phases are associated with geographic distribution, for all of them have been taken together at the same localities. For this reason no varietal name is given to the color extreme opposite that illustrated by Beauvois.

The type of this species, together with the types of many other hymenopterous species of Beauvois, seems to be lost. Some of this author's

coleopterous types are in the British Museum, but no one has yet discovered the whereabouts of the others. It seems advisable, therefore, to erect neo-types for the two Nearctic species, *D. unicolor* and *D. bicolor*.

Dolerus borealis MacGillivray

Dolerus borealis MacGillivray, Can. Ent., Vol. XXV, No. 10, Oct., 1893, p. 238; Frison, Bull. Ill. Nat. Hist. Surv., Vol. XVI, Art. IV, Feb., 1927, p. 240.

Dolerus nominatus MacGillivray, Ins. Insc. Mens., Vol. XI, Nos. 1-3, 1923, p. 34; Frison, Bull. Ill. Nat. Hist. Surv., Vol. XVI, Art. IV, Feb., 1927, p. 240. *New synonymy*.

Female.—Length 9 mm. Color black, with the lateral lobes rufous. Wings fuliginous-hyaline.

Head reticulately punctate, with a small impunctate or shagreened area on postocular area near lateral ocellus; postocular area, seen from above, distinctly longer than eye, corners rounded; posterior margin of head almost transverse, with a small but distinct ridge; postocular area with a wide, rounded, transverse carina; vertical furrows distinct, wide near ocelli, narrowing to a line at posterior margin; postocellar area one and one-half times wider than long, shining, with large punctures; flagellum of antennae very slender, third and fourth antennal segments sub-equal, the others very gradually decreasing towards apex. Disk of anterior lobe shining, only obscurely punctate, lateral areas finely but roughly punctate, the lateral areas only half as wide as complementary portion of disk; lateral lobes shining, sparsely punctate; post-tergite triangular, only obscurely striate, meson round-carinate, posterior margin angular; pleurae and pectus as in *neocollaris*. Sheath thin and blade-like (Figure 24), setae short and slender, very slightly tufted at apex; saw very similar to *neocollaris* (Figure 43), but with only 17 lobes, each one slightly longer and with more numerous, finer teeth.

Male.—Unknown for certain, but perhaps *nativus* MacG., which occurs in the same region, and agrees very well in structure with *borealis*. There exists a great color diversity between the two, but that does not necessarily bar them from being the same species.

Holotype.—♀, Olympia, Washington, May 22, 1892 (T. Kincaid). In the MacGillivray Collection, University of Illinois, Urbana, Ill.

Distribution.—Known from only two specimens besides the type, namely, one female, Moscow, Idaho (J. M. Aldrich), and one female, Oregon, the type of *nominatus* MacG. This specimen differs from the typical specimen only in having the upper part of the pleurae rufous.

This rare and handsome species is easily recognized by its unique coloration.

Dolerus nativus MacGillivray

Dolerus nativus MacGillivray, Ins. Insc. Mens., Vol. XI, Nos. 1-3, 1923, p. 32; Frison, Bull. Ill. Nat. Hist. Surv., Vol. XVI, Art. IV, Feb., 1927, p. 242.

Dolerus nectareus MacGillivray, Ins. Insc. Mens., Vol. XI, Nos. 1-3, 1923, p. 33; Frison, Bull. Ill. Nat. Hist. Surv., Vol. XVI, Art. IV, Feb., 1927, p. 242. *New synonymy*.

Male.—Length 8 mm. Head and thorax entirely black; abdomen rufous except segments 7 and 8 which are black. Wings brownish infusate, fairly deeply so at base, but lighter towards apex.

Structurally similar to *borealis*. It also agrees quite closely with *interjectus* Ross, a member of the *bicolor* group, from which it differs as follows: pubescence less dense, postocular area with a fairly large shagreened area without punctures; lateral lobes very shining; pectus highly polished, minutely punctured; hypopygium with the apex more rounded, the posterior margin and sides meeting to form a rounded shoulder. Genitalia agreeing in proportion with Figure 67, but with the praeputium not sharply concave and with the gonocardo as in Figure 66.

Female.—See remarks under *borealis* regarding the male.

Holotype.—♂, Entermille, Oregon, April, 29, 1917 (Baker). In the MacGillivray Collection, University of Illinois, Urbana, Ill.

Distribution.—As in the case of *borealis*, very rare: COLORADO: 1♂, "Col." (Coll. A. N. S. Phil.). OREGON: 1♂, Entermille, Apr. 29, 1917 (Baker). This latter specimen is the type of *nectareus* MacG. It differs from the type of *nativis* in having the postocular area, disk of anterior lobe and post-tergite more or less shagreened.

This species differs from *interjectus* by characters given in the description, and from many members of the *similis* group, which it greatly resembles and with which it is likely to be confused, by the finely punctured pleurae which merge so smoothly and imperceptibly with the pectus and by characters of the genitalia.

Dolerus illini new species

Female.—Length 9 to 11 mm. Color mostly black, with the pronotum, anterior lobe and upper half of meso-episternum rufous. In most specimens the head has an indistinct bluish reflection, in some the lateral lobes are rufous, and a few have the thorax almost entirely black except for indistinct rufous areas at the corners of the pronotum and anterior lobe. Front wings slightly brownish-gray infusate, hind wings almost hyaline.

Head rather smoothly, reticulately punctate, with a small shagreened area postero-laterad of lateral ocelli; clypeus more or less angularly notched for one-third its length; seen from above postocular area longer than eye, robust, very slightly expanded behind eye, the posterior margin lacking a carina, the caudo-lateral corners somewhat quadrate; posterior margin of head slightly immarginate; vertical furrows deep and trenchlike, but only reaching two-thirds of the distance to the posterior margin; postocellar area quadrate, raised above the level of the postocular area, which is uniformly flat; in most specimens of this species the median fovea is a minute shining spot in the bottom of a punctate depression, and the ocellar fovea is a small polished spot adjacent to and in front of the median ocellus; ocellar basin

obsolete; antennae moderately thick, third segment longer than fourth, the remainder gradually decreasing in length. Anterior lobe sub-inflated, disk shining, minutely punctate, lateral areas with even, more or less distinct punctures; lateral lobes shining, with moderately dense but small punctures; post-tergite polished, flat and triangular, at most only obscurely striate at base, mesal portion bevelled but not carinate, posterior margin very bluntly angled, scarcely crescentic; mesopleurae smoothly pitted, the walls of the punctures glossy and rounded; pectus polished, minutely punctured, with a diagonal linear strip of denser, larger punctures. Sheath as in Figure 23, blade-like, the apical portion with a very narrow, uniform scopa; sides of sheath shagreened; setae suggestive of the *bicolor* group, most of the setae being short, in a uniform series, but with a small number near the caudo-ventral angle about twice as long as the others; setae brown; cerci half dorsal length of sheath; saw as in Figure 45; lance with about 23 segments, the tip serrate; lancet with about 19 segments, the annuli represented by oblique bands of minute spines, lobes with about eight fine, even teeth.

Male.—Length 9 to 10 mm. Color entirely black, except head, which usually has the dorsal portion bluish-black. Front wings very faintly tawny, hind wings hyaline.

Structure very similar to female. Differs as follows: first three segments of flagellum either subequal, or the second slightly the longest; pleurae more finely punctured. Ninth tergite one-third length of eighth; hypopygium long, sides of apex not so convergent as in *neocollaris*, the posterior margin sub-truncate. Genitalia as for group (Figure 65).

Holotype.—♀, Seymour, Illinois, April 14, 1929 (Park and Ross). Deposited in the collection of the Illinois State Natural History Survey, Urbana, Ill.

Allotype.—♂, same data as holotype, and deposited with it.

Paratypes.—COLORADO: 1♂, Fort Collins, May 5, 1900; 1♂, Mineral County, June 20, 1919, 10,800 ft. alt. CONNECTICUT: 1♀. ILLINOIS: 62♂♂, 68♀♀, Seymour, Apr. 14, 1929 (Park and Ross); 10♂♂, 13♀♀, Seymour, Apr. 15, 1929 (Frison and Ross); 4♀♀, Bondville, Apr. 15, 1929 (Frison and Ross); 1♂, 2♀♀, Galton, Apr. 18, 1929 (Frison and Ross); 1♂, White Heath, Apr. 15, 1929 (Frison and Ross); 2♂♂, 6♀♀, Thomasboro, Apr. 24, 1929 (Frison and Ross); 1♂, 3♀♀, St. Joseph, Apr. 16, 1929 (Frison and Ross); 5♂♂, 3♀♀, Urbana, Apr. 16, 1929 (Frison and Ross); 2♂♂, 2♀♀, Ogden, Apr. 16, 1929 (Frison and Ross); 1♂, 2♀♀, Chebanse, Apr. 24, 1929 (Frison and Ross); 2♂♂, Paxton, Apr. 24, 1929 (Frison and Ross); 18♀♀, Ludlow, Apr. 24, 1929 (Frison and Ross); 1♀, Tolono, Apr. 18, 1929 (Frison and Ross); 6♀♀, Rantoul, Apr. 24, 1929 (Frison and Ross); 1♀, Seymour, Apr. 17, 1929 (H. H. Ross); 1♀, Algonquin, Apr. 25, 1894 (W. Nason); 10♂♂, 12♀♀, Snyder, April 16,

1930 (Frison and Ross). IOWA: 1 ♀, Ames, Apr. 26, 1926 (G. Hendrickson); 1 ♀, Ames, May 5, 1926 (G. Hendrickson). KANSAS: 1 ♀, Lawrence, Apr. 18, 1923 (W. G. Garlick); 1 ♂, Douglas County, 1920 (W. E. Hoffman); 4 ♂♂, Douglas County, April. MASSACHUSETTS: 1 ♀, Saugus, Apr. 29, 1920 (C. E. Hofer); 1 ♀, Stoneham, Jn. 1, 1920 (C. E. Hofer); 1 ♂, Chicopee, May 17, 1902; 1 ♀, Forest Hills, May 1, 1917 (A. M. Wilcox); 1 ♀, Longmeadow, May 14, 1905 (F. K. Knab); 1 ♀, Tynsboro, (F. Blanchard); 1 ♀, Bedford, May 4. MICHIGAN: 2 ♀♀, Ann Arbor, May 22, 1919 (T. H. Hubbell); 1 ♀, Ann Arbor, May 18, 1919 (T. H. Hubbell); 1 ♀, Ann Arbor, Apr. 18, 1917; 1 ♂, Ag. Coll. NEW HAMPSHIRE: 1 ♀, Franconia; 1 ♀, N. H., 1879. NEW JERSEY: 1 ♀, Ramsey, Apr. 30, 1911. NEW YORK: 1 ♀, Ithaca, Apr. 20, 1895; 1 ♀, Ithaca, May, 1893. SOUTH DAKOTA: 4 ♀♀, S. D.; 3 ♀♀, Brookings; 1 ♀, Brookings, Jn. 12, 1923 (H. C. Severin). ALBERTA: 1 ♂, Gull Lake, Ap. 4, 1929 (E. H. Strickland); 1 ♀, Gull Lake, Jn. 8, 1929 (E. H. Strickland). MANITOBA: 1 ♀, Birtle, May 25, 1928 (R. D. Bird). Deposited in a large number of collections.

In the vicinity of Urbana, Ill., this species was taken in great abundance in the Equisetum, Eleocharis and Carex habitats similar to Figure 72. It was one of the earliest species to reach its greatest abundance in this habitat, attaining its peak at the same time as *aprilis* and *agcistus*.

The female of *illini* can be separated from other species of the same color by the long, thin sheath and the saw. Both sexes differ from *neocolaris* in the shorter and more robust postocular area, and from similarly colored members of the *bicolor* group by the more quadrate head, having the anterior lobe slightly wider and shorter with the disk polished, and the polished pectus and post-tergite. The female of *tectus* differs in having a shorter, shouldered saw (Figure 17), the male in having a crescentic, not triangular, post-tergite, and more sparsely punctured lateral areas of the anterior lobe.

Dolerus illini var. *rufilobus* new variety

Male.—Color black, except for the collar, anterior lobe, and extreme upper corner of meso-pleurae, which are rufous. In other respects precisely as in the typical form of the species.

Holotype.—♂, Brookings, South Dakota. In the collection of the Illinois State Natural History Survey, Urbana, Ill.

Known only from the type. This variety can be separated from the males of all other species of the genus by its color. It is a male which apparently has assumed the same coloration as the female.

Dolerus tectus MacGillivray

Dolerus tectus MacGillivray, Can. Ent., Vol. XLVI, No. 3, Mar., 1914, p. 104; MacGillivray, Bull. 22, Conn. Geol. Nat. Hist. Surv., 1916, p. 70; Frison, Bull. Ill. Nat. Hist. Surv., Vol. XVI, Art. IV, Feb., 1927, p. 244.

Female.—Length 9 to 10 mm. Color entirely black. Wings uniformly faintly tawny.

Structurally extremely similar to *illini*, differing as follows: punctuation of head slightly coarser, postocular area a trifle more convex; post-tergite polished, crescentic, posterior margin circularly rounded, median length small, dorsal surface convex, but not approaching carinate; sheath (Figure 17) caudo-ventrally shouldered, not evenly rounded as in *illini*, setae similar to the latter, with a number of longer ones on the caudal margin; saw differs only in having more teeth on the lobes, averaging ten instead of eight.

Male.—Length 8.5 to 9.5 mm. Color entirely black, wings slightly tawny.

Structurally similar to male of *illini*, from which it differs as follows: post-tergite crescentic, not triangular, the posterior margin circular, not angular; anterior lobe with punctures on lateral areas more widely separated, and with more punctures on the posterior corner; anterior angles of lateral lobes a trifle shagreened; posterior margin of hypopygium circularly rounded.

Holotype.—♀, New Haven, Connecticut, May 4, 1904, on *Salix* (H. L. Vierick). In the MacGillivray Collection, University of Illinois, Urbana, Ill.

Lectoallotype.—♂, same data as holotype. Labeled as a paratype by MacGillivray but not mentioned in the original description (Frison, 1927). Present designation.

Distribution.—♂, ♀, New Haven, Conn., (types); 1 ♀, Chelsea, Mass., April 21; 1 ♀, Ann Arbor, Mich., May 13, 1919 (T. H. Hubbell); 1 ♀, Brookings, S. D.

A rare species of scattered distribution. It is most closely allied to *illini*, but can be separated from it by characters listed in the description. The sheath, postocular area and pectus, together with the very rotund hind tibiae, will separate it from members of the *sericeus* group, with which it has usually been confused.

SERICEUS GROUP

Usually large black species; clypeus only moderately cleft, less than one-half its length, the cleft V-shaped, the lobes angular; head below vertex closely reticulate; vertical furrows very deep and distinct, making the postocellar area extremely well set out; third antennal segment almost equal to fourth, but slightly longer, the following segments very gradually diminishing in length; flagellum setaceous, slightly narrowed towards tip. Punctuation of thorax variable; post-tergite usually shining, variable in shape; pectus very distinctly set off from pleurae, usually shagreened and punctate, with a distinct diagonal row, pectus more or less concave between

diagonal row and pleurae; hind tibiae distinctly longitudinally grooved on both inner and outer sides; claws with a tooth. Females with a thin, blade-like sheath without a scopa, saws of all the forms very similar. Males with a distinct median procidentia on the posterior margin of the eighth tergite. Genitalia as in Figure 66; praeputium long, angular at base and with finger-like apices; gonocardo very narrow, constricted on the meson; pedes small.

Dolerus sericeus Say *sens. lat.*

This species complex presents a multitude of variations in the polish of the vertex, the relative size and numbers of the punctures of the anterior lobe, meso-episternum and pectus, the shape of the post-tergite, in the female the shape of the sheath, and in the male the shape of the procidentia. Some of these variations can be separated into groups which have been considered as species by some authors, but the differences are so variable and so essentially a matter of comparative degree that it is impossible to give a key for the satisfactory treatment of all specimens of the complex. It suggests very strongly a species in the active process of evolution. It is possible to delineate two or three groups, termed subspecies in this paper, which possess fairly constant characteristics, differing from each other in a comparative degree. It is not always possible to assign a specimen to a definite race. Whether these subspecies represent good species, or are all merely variations of the same species, is a matter of conjecture, which will probably be settled only by breeding experiments.

The following is a key to the subspecies of *Dolerus sericeus* Say:

1. Females.....2
- . Males.....5
2. Sheath relatively narrow and pointed, as in Figure 19, dorsal margin convex at tip; sides of anterior lobe with a few large, crater-like punctures; pectus usually with conspicuous scattered punctures.....*sericeus* subsp. *centralis* Ross
- . Sheath wider, dorsal margin straight or concave.....3
3. Sides of anterior lobe more or less uniformly reticulate, not with at least four or five large, crater-like punctures; lateral areas of pectus very opaque, densely shagreened, usually with only very minute punctures.....*sericeus* Say *s. st.*
- . Sides of anterior lobe with at least five or six large crater-like punctures conspicuously larger than the rest.....4
4. Punctures of meso-episternum of medium size; pectus inclined to shining, diagonal row of punctures not conspicuously large or rough, lateral portion not strongly concave, usually only slightly shagreened; smaller, 9 to 11 mm.
.....*sericeus* subsp. *parasericeus* MacG.
- . Punctures of meso-episternum very large and deeply impressed; pectus dull, diagonal row and median punctures conspicuously coarse, with rough walls, lateral portion strongly concave, very densely shagreened; larger, 11 to 12 mm.
.....*sericeus* subsp. *neosericeus* MacG.
5. Pectus dull, entirely shagreened, without any shining areas.....6
- . Pectus slightly shining, sometimes slightly shagreened, but always with a gloss on the lateral areas.....7

6. Sides of anterior lobe and meso-episternum with large, crater-like punctures; pectus with diagonal row of punctures conspicuously coarse, walls rough; procidentia low, round and knob-like, base sometimes carinate. *sericeus* subsp. *neosericeus* MacG.
- Sides of anterior lobe evenly reticulately punctured; meso-episternum only moderately coarsely punctured; pectus quite smoothly punctured, diagonal row moderately fine; procidentia inverted trough-like, fairly high, ridge-like for its entire length
. *sericeus* Say s. st.
7. Procidentia one-half length of eighth tergite, carinate for its whole length, dorsal edge slightly depressed near middle. *sericeus* subsp. *parasericeus* MacG.
- Procidentia one-quarter length of eighth tergite, small, rounded and drop-like, with a faint indication of a carina at its base. *sericeus* subsp. *centralis* Ross

Dolerus sericeus Say sens. st.

Dolerus sericeus Say, Keatings Narrat. Exped. II, 1824, App., p. 320; Leconte, Writ. Thomas Say Entom., II, 1859, p. 214; Norton, Proc. Boston Soc. Nat. Hist., Vol. VIII, 1861, p. 154; Norton, Trans. Amer. Ent. Soc., Vol. I, 1867, p. 235; Provancher, Nat. Canad., Vol. X, 1878, p. 71; Provancher, Faun. Ent. Can., Hymen., 1883, p. 197; Dalla Torre, Cat. Hymen., Vol. I, 1894, p. 17; MacGillivray, Bull. 22, Conn. Geol. Nat. Hist. Surv., 1916, p. 69.

Dolerus colosericeus MacGillivray, Can. Ent., Vol. XL, No. 4, April, 1908, p. 125; MacGillivray, Bull. 22, Conn. Geol. Nat. Hist. Surv., 1916, p. 70; Frison, Bull. Ill. Nat. Hist. Surv., Vol. XVI, Art. IV, Feb., 1927, p. 240. *New synonymy.*

Dolerus monosericeus MacGillivray, Can. Ent., Vol. XL, No. 4, April, 1908, p. 126; Frison, Bull. Ill. Nat. Hist. Surv., Vol. XVI, Art. IV, Feb., 1927, p. 241. *New synonymy.*

Female.—Length 10 to 11.5 mm. Color entirely black. Front wings uniformly dark brown, hind wings uniformly a lighter brown.

Head as for group; postocular area as long as eye, seen from above, dull, with reticulate punctures and shagreening on the unpunctured areas, with a low, narrow, transverse carina somewhat obscured by it dense punctuation, posterior margin with a coarse carina; postocellar area quadrate, raised above level of postocular area, more or less shining and punctate. Disk of anterior lobe shining and evenly punctured, sides fairly evenly reticulate with more or less elongate punctures, not round, smaller than in the other species, only occasionally with one or two punctures conspicuously larger than the rest; lateral lobes evenly punctured, shining or more or less shagreened; post-tergite smooth, with or without a rounded median carina, posterior margin more or less triangular; meso-episternum with irregular reticulate punctures, not very large, with a smooth appearance; pectus shagreened, finely and minutely punctured, diagonal row of sparse, small punctures; punctuation of legs very fine and minute. Sheath long and blade-like, much as in Figure 20, but narrower, the dorsal margin straight or very slightly convex (Figure 21), the ventral margin evenly arcuately rounded, scopa lacking; setae in an evenly graduated series, not very long or coarse; cerci short, only about a quarter of dorsal length of sheath.

Male.—In size, color and structure similar to female, with the following differences in structure: meso-episternum slightly less roughly reticulate;

hypopygium very convex, long, apex with sides straight and oblique, posterior margin truncate; procidentia tent-like, more or less half length of eighth segment, meson carinate, the top of the ridge straight not concave.

Neotype.—♀, Philadelphia, Pennsylvania, May 10, 1887. In the collection of the Illinois State Natural History Survey, Urbana, Ill.

Distribution.—DELAWARE: 1♂, Del. ILLINOIS: 1♂, 1♀, Palos Park, Apr. 24, 1930 (Frison and Ross). INDIANA: 1♀, LaFayette (F. M. Webster). MAINE: 1♂, Orono. MASSACHUSETTS: 5♂♂, 1♀. Chelsea Bay, April 21; 1♂, Amherst, April 21, 1908. MINNESOTA: 1♀ St. Anthony Pk. MISSOURI: 1♀, "Mo." NEW JERSEY: 2♂♂, N. J. NEW YORK: 3♂♂, 4♀♀, Ithaca, Apr. to May 12; 1♀, Nassau, May 16, 1906; 1♀, Albany, Apr. 15, 1910; 1♂, Staten Island; 1♀, Syracuse, Apr. 20, 1924. PENNSYLVANIA: 3♀♀, Pa. RHODE ISLAND: 1♀, Kingston, Apr. 30, 1905. BRITISH COLUMBIA: 1♂, Vernon, Apr. 25, 1919 (N. W. Ruhmann). ONTARIO: 1♂, Ottawa, Apr. 27, 1921 (J. McDunnough); 1♂, Ottawa, May 17, 1914 (A. E. Kellett); 1♂, Hastings County; 1♀, Sudbury; 1♀, Jordan, Jly. 12, 1920 (W. A. Ross); 1♀, Jordan, Apr. 5, 1915. QUEBEC: 1♂, Lake Opasatika, Jn. 10, 1921 (H. S. Fleming); 1♂, Lake Opasatika, Jn. 1 (J. N. Knull); 1♀, cottage Beaulieu, Jn. 29, 1904.

Judging from its distribution, this is the form studied by Norton (1867). It is also the one referred to by MacGillivray (1916) as his identified specimens show. This is the form of *sericeus* most commonly taken in the eastern states. Its salient characters are: the sides of the anterior lobe fairly uniformly reticular-punctate with at most one or two larger punctures; the post-tergite usually fairly long, flattish and sub-triangular; the pectus dull, densely shagreened, the lateral areas only minutely punctured, the diagonal row not coarse or conspicuously large; the female with the sheath having the ventral margin evenly rounded, the dorsal margin straight or concave, the tip arc-shaped, never truncate (Figure 21), the sides shagreened; the male with the procidentia long and ridge-like, inverted trough-shaped.

Dolerus sericeus subsp. *parasericeus* MacGillivray.

Dolerus parasericeus MacGillivray, Can. Ent., Vol. XL, No. 4, April, 1908, p. 125; MacGillivray, Bull. 22, Conn. Geol. Nat. Hist. Surv., 1916, p. 69; Frison, Bull. Ill. Nat. Hist. Surv., Vol. XVI, Art. IV, Feb., 1927, p. 244.

Dolerus polysericeus MacGillivray, Can. Ent., Vol. XL, No. 4, April, 1908, p. 125; MacGillivray, Bull. Conn. Geol. Nat. Hist. Surv., 1916, p. 70; Frison, Bull. Ill. Nat. Hist. Surv., Vol. XVI, Art. IV, Feb., 1927, p. 244. *New synonymy*.

Female.—Similar in size and color to *sericeus s. st.* Differs in structure in having six to twelve round, crater-like punctures on sides of anterior lobe conspicuously larger than the rest; meso-episternum with larger, rounder punctures; pectus usually shining, sometimes partly shagreened, the diagonal row distinct, of somewhat scattered, large punctures; post-

tergite variable; sheath resembling the typical form, but slightly more truncate, with the dorsal margin always straight (Figure 20); saw as in *sericeus s. st.* (Figure 46), without annuli.

Male.—Similar in structure to female. Procidentia very similar to *sericeus s. st.*, but differs very slightly in having the dorsal ridge slightly depressed near the middle. It differs from the typical form chiefly in the lesser shagreening of the pectus.

Holotype.—♀, Ithaca, New York, June 17, 1897. In the MacGillivray Collection, University of Illinois, Urbana, Ill.

Allotype.—♂, Victoria, British Columbia, April 23, 1919 (W. Downes). Deposited in the Canadian National Museum, Ottawa, Canada. Present designation.

Distribution.—NEW YORK: Holotype, Ithaca. BRITISH COLUMBIA: Allotype, Victoria; 1 ♀, Agassiz, Jn. 15, 1926 (H. H. Ross); 2 ♀ ♀, Agassiz, Apr. 26 and 28, 1927 (H. H. Ross); 1 ♀, Agassiz, May 8, 1927 (H. H. Ross).

This form is separated from *sericeus s. st.* and from subsp. *neosericeus* by its shining pectus, and from subsp. *centralis* by the sheath in the female and the procidentia in the male.

Dolerus sericeus subsp. *centralis* new subspecies

Female.—Length 9 to 11 mm. Color entirely black, wings brownish-infusate.

Structure typical for the group. Head coarsely punctate, postocular area particularly so; postocular area shorter than eye, seen from above, narrowed behind eye, with a transverse carina almost obscured by the large coarse punctures, median portion shining, posterior margin with a carina; vertical furrows very wide and deep; postocellar area quadrate, convex and shining, sparsely punctured. Halves of anterior lobe only moderately convex; sides rugose, usually with a few large punctures, but not as regularly circular as in subsp. *parasericeus*, but much rougher than in the typical *sericeus*; disk and lateral lobes densely, evenly punctured; posttergite sub-triangular, shining, sometimes faintly striate; meso-episternum rugose-reticulate, punctures uneven; pectus lightly shagreened, glossy but not polished, lateral areas and diagonal row comparatively densely punctate. Sheath narrow (Figure 19), dorsal margin more or less convex, especially at apex, apex biconvexly pointed.

Male.—Similar in size, color and structure to female. Procidentia small, round and knob-like, only one-quarter length of eighth tergite.

Holotype.—♀, Urbana, Illinois, April 22, 1929 (T. H. Frison). Deposited in the collection of the Illinois State Natural History Survey, Urbana, Ill.

Allotype.—♂, Augerville Woods, Urbana, Illinois, April 21, 1920 (T. H. Frison). Deposited with the holotype.

Paratypes.—2 ♀ ♀, Augerville Woods, Urbana, Ill., Apr. 29, 1920 (T. H. Frison); 1 ♀, Urbana, Ill., sweeping, Apr. 24, 1924 (T. H. Frison); 1 ♂, Cottonwoods, Urbana, Ill., Apr. 18, 1918; 1 ♀, Oakwood, Ill., May 8, 1920 (T. H. Frison); 1 ♀, Champaign, Ill., May 3, 1912 (T. H. Frison); 1 ♀, White Heath, Ill., Apr. 23, 1917; 3 ♀ ♀, Urbana, Ill., Apr. 29, 1928 (A. R. Park); 1 ♂, Decatur, Ill., May, 1905, frequenting peony buds (Taylor) (34944); 1 ♀, Putnam, Ill., May 5, 1929 (T. H. Frison). Deposited in the collections of Dr. T. H. Frison, the Illinois State Natural History Survey, Mr. A. R. Park and the author.

This subspecies has so far been taken only in Illinois. It differs from *sericeus s. st.* and from subsp. *neosericeus* in the lighter shagreening of the pectus. The female can be distinguished by the narrower and more pointed sheath, and the male can be separated from *sericeus s. st.* and subsp. *parasericeus* by the round procidentia and from subsp. *neosericeus* by the shining pectus and smaller size.

Dolerus sericeus subsp. *neosericeus* MacGillivray

Dolerus neosericeus MacGillivray, Can. Ent., Vol. XL, No. 4, April, 1908, p. 125; MacGillivray, Bull. 22, Conn. Geol. Nat. Hist. Surv., 1916, p. 69; Frison, Bull. Ill. Nat. Hist. Surv., Vol XVI, Art. IV, Feb., 1927, p. 242.

Dolerus necosericeus MacGillivray, Univ. Ill. Bull., Vol. XX, No. 50, Aug. 13, 1923, p. 13; Frison, Bull. Ill. Nat. Hist. Surv., Vol. XVI, Art. IV, Feb., 1927, p. 242. *New synonymy.*

Female.—Length 10.5 to 13 mm. Color black, wings brownish infusate.

Differs from the typical *sericeus* as follows: postocular area more robust and shining; sides of anterior lobe with several very large, round punctures very conspicuously larger than the others; pleurae with very large, more or less equal punctures, deeply hollowed out; pectus densely shagreened, markedly depressed between the pleurae and the diagonal row, coarsely and unevenly punctured, the diagonal row consisting of large, closely-set punctures; sheath long (Figure 18), somewhat truncate as in subsp. *parasericeus*, with the dorsal margin slightly convex, the sides shining, not shagreened; the saw almost as in the other forms, but with the teeth twice as large as those in *sericeus s. st.*, subsp. *parasericeus* or subsp. *centralis*.

Male.—Similar in size, color and structure to female. Procidentia low, rounded and knob-like at apex, with a low, carinate extension at base.

Holotype.—♀, Ithaca, New York. In the MacGillivray Collection, University of Illinois, Urbana, Ill.

Allotype.—♂, Mt. Washington, Massachusetts, Deposited with the holotype. Present designation.

Distribution.—MAINE: 1 ♀, Orono, Jly. 3, 1913. (Type of *necosericeus*). MASSACHUSETTS: 1 ♂, Mt. Washington; 1 ♀, Green Lodge, Jn. 17, 1905; 1 ♀, Lexington, May. MICHIGAN: 1 ♀, South Haven, Jn. 1, 1891. NEW HAMPSHIRE: 3 ♀ ♀, Jefferson, Jn. 14, 1895; 1 ♀, Fran-

conia. NEW YORK: 1♂, 1♀, Utica; 1♀, Caatskill Mts., Jn. 25, 1904. WISCONSIN: 1♀, Cranmoor, Jn. 6, 1910 (C. W. Hooker). NEW BRUNSWICK: 3♀, Bathurst, Jly. 6. ONTARIO: 1♀, Bondville, Jn. 26, 1913 (W. A. Ross).

This subspecies is the largest and most coarsely punctured in the group. It is easily recognized in both sexes by the combination of the large punctures on the anterior lobe and pleurae and the densely shagreened pectus with the heavy diagonal row.

BICOLOR GROUP

Size and color various; mesopleurae usually finely, always evenly, punctate; pectus sparsely punctate, shining or shagreened; posterior tibiae not grooved on outer side, at most grooved very slightly on inner; sheath with a distinct scopa or thickened, truncate caudal margin (except in *nortoni*), the scopa being more definite in the species in which it is narrow, the edge often becoming rounded when it is wide, giving the sheath the appearance of a barrel; male genitalia short and wide (Figure 67); praeputium markedly transversely concave in most specimens, but sometimes scarcely concave at all; gonocardo wider than in *sericeus* or *unicolor*, distinctly clavate laterally; pedes various.

Dolerus versa Norton

Dolerus versa Norton, Trans. Amer. Ent. Soc., Vol. I, 1867, p. 239; Dalla Torre, Cat. Hymen., Vol. I, 1894, p. 19; MacGillivray, Bull. 22, Conn. Geol. Nat. Hist. Surv., 1916, p. 74; Cresson, Mem. Amer. Ent. Soc., No. 5, 1928, p. 10.

Female.—Length 11 to 12 mm. Color: head black; thorax black with the prothorax, tegulae, lateral lobes, upper and upper caudal portion of meso-episternum, dorsal sclerite of meso-epimeron, more or less of the ventral portion of the meso-epimeron, the metapleurae entirely or partly, and the basal plates, rufous; lateral margins of anterior lobe also sometimes rufous; abdomen rufous, except cerci sometimes, sheath and external basal portion of the gonapophyses, which are black. Wings uniformly deeply infusate with brownish-violaceous, slightly deeper towards base.

Head quadrate seen from above, eyes prominent; corners square, posterior margin uniformly arcuately emarginate; length of postocular area subequal to length of eye, seen from above, with an indistinct carina on posterior margin visible only near mesal portion, and with a low, rounded transverse ridge across the dorsum; vertical furrows very deep and pit-like, separated by a thick wall from posterior margin of head; postocellar area subquadrate, raised slightly; lateral ocelli equidistant from each other and posterior margin of head; vertex shining, with large, sparse punctures; front and lower parts of head quite finely, reticulately punctate; third segment of antennae only slightly longer than fourth, remainder diminishing

very gradually. Mesonotum shining; anterior lobe uniformly convex, disk with shallow, fairly sparse punctures, sides with large, sparse punctures with rounded, polished sides; lateral lobes with sparse, shining punctures; post-tergite shallowly U-shaped, densely striate, opaque, with a sharp median carina ending before the apex, which is almost truncate; meso-episternum very coarsely, but evenly, punctate, the bottom of the punctures shining; pectus faintly shagreened, very sparsely punctate except for a diagonal row of denser punctures. Sheath as in Figure 25, triangular, blade-like and pointed, with a very narrow, distinct scopa; the longer setae pointing almost directly laterad; cerci attaining almost tip of sheath; saw simple, annuli distinct, lones plainly toothed, very rudimentary spurettes present on apical portion (Figure 48).

Male.—Length 9 to 10 mm. Color and structure identical with female. Ninth tergite scarcely visible, hypopygium short, apical lateral margins slightly concave, posterior margin sub-truncate.

Lectotype.—♀, Massachusetts. In the collection of the Philadelphia Academy of Natural Sciences, Philadelphia, Pa. (Cresson, 1928).

Distribution.—MARYLAND: 1♂, Prince-George County, Jn. 28; 1♀, Prince George County, Apr., 1896. MISSOURI: 1♂, St. Louis, 1877; 1♀, Mo. NEW JERSEY: 1♂, Lakehurst, April 30, 1916; 1♂, N. J. NEW YORK: 1♀, New York City. OHIO: 1♀, Columbus, Apr. 21, 1920 (A. E. Miller); 4♀♀, Hocking County, May (C. H. Kennedy); 1♀, Jacko County, May, 1926. PENNSYLVANIA: 13♂♂, Highspire, Jn. 17, 1909 (W. S. Fisher); 1♀, Delaware County, Apr. 22, 1894 (C. W. Johnson). DISTRICT OF COLUMBIA: 1♀, D. C., May 5. VIRGINIA: 1♂, Vienna, May 9, 1911; 3♀♀, Falls Church, Apr. 25.

This large species may be confused with *piercei*, but can be readily separated by the darker wings and coarser punctuation of the anterior lobe.

Dolerus piercei Rohwer

Dolerus Piercei Rohwer, Can. Ent., Vol. XLI, No. 1, Jan., 1909, p. 10.

Female.—Length 8 to 9.5 mm. Head black; thorax rufous with median half of anterior lobe, lateral lobes sometimes, scutellum and post-tergite, metanotum except basal plates, pectus and lower portion of meso-episternum, and legs, black; abdomen rufous with sheath and cerci black. Wings uniformly light tawny infuscate.

Structure differing from *versa* only in the smaller punctures on the head and thorax, and in the slightly more rounded corners of the head. Punctuation of head almost uniform; punctures of postocular area little larger than those of front, but sparser; transverse ridge lacking. Anterior lobe opaque with punctures, those on disk minute and dense, those on sides rough and dense; pleurae finely and evenly punctate; pectus shining, finely punctate.

Sheath similar to *versa*; saw (Figure 61) similar in outline, but differing in having small, peg-like spurettes and alar spurs.

Male.—Unknown.

Type.—♀, Lincoln, Nebraska, April 19, 1902, "Immodelle" (W. D. Pierce). In the collection of the University of Nebraska Lincoln, Nebr.

Distribution.—KANSAS: 1 ♀, Douglas Co., Apr., 1923 (R. H. Beamer). NEW JERSEY: 1 ♀, South Seaville, May 25, 1923 (J. C. Bradley).

This rare species may be distinguished from *versa* by the finer punctuation of the anterior lobe and meso-episternum. The specimens with the lateral lobes rufous may be distinguished from *clypealis*, *collaris*, etc., by the black mark on the anterior lobe; the specimens with the lateral lobes black can be distinguished from *clypealis*, *collaris*, etc., by the triangular saw with the small, peg-like alar spurs and spurettes.

Dolerus clypealis new species

Female.—Length 7.5 to 9.5 mm. Head black, with the clypeus entirely or with the apical half rufous; thorax rufous with the metanotum, except basal plates, pectus and legs except front knees, rufous; sometimes with a black spot on lateral lobes or with scutum black; abdomen rufous with sheath black. Wings almost hyaline, with a very slight yellowish staining.

Head uniformly, finely punctate, except ridge of postocular area which is partly impunctate and shagreened; postocular area robust, corners rounded, seen from above slightly longer than eye, possessing a low, transverse ridge, posterior margin not carinate; posterior margin of head shallowly evenly emarginate; vertical furrows elongate pit-like, reduced to a line at posterior margin; postocellar area one and one-half times as wide as long, slightly raised above level of postocular area; median and ocellar foveae obsolete; third segment of antennae slightly but distinctly constricted just above base, ventral side arcuate, fourth segment narrower at base, gradually widening towards apex, a fourth shorter than third, the remaining segments scarcely diminishing in length. Halves of anterior lobe uniformly convex, disk shining, moderately densely and finely punctate, lateral areas opaque with slightly coarser and much denser punctures; lateral lobes shining, sparsely punctured; post-tergite subtriangular, finely striate, appearing shining when rufous, mesally carinate, posterior margin angulate, extreme tip rounded; pleurae finely reticulately punctate, dull, pectus shining, with many fine punctures; tarsal claws with a small triangular tooth. Sheath as in Figure 25, thin and triangular, apex pointed, the longer setae very divergent; scopa narrowly ellipsoidal, as in *versa*; cerci attaining apex of sheath; saw subtriangular (Figure 49); lance with about 10 segments, the dorsal margin at apex scalloped or broadly serrate; lancet with about 11 segments, ventral margin concave, the lobes coarse and prominent, annuli distinct, with rudimentary spurettes, rudimentary alar spurs sometimes also present; annuli without spines.

Male.—Not recognized. Most likely similar to and difficult to separate from that of *collaris*, etc.

Holotype.—♀, Gull Lake, Alberta, Canada, June 25, 1929 (E. H. Strickland). In the collection of the Illinois State Natural History Survey, Urbana, Ill.

Paratypes.—Mon. COLORADO: 2 ♀ ♀, Garland; 1 ♀, Westcliff. MONTANA: 5 ♀ ♀, UTAH: 1 ♀, Park City, June 18. ALBERTA: 4 ♀ ♀, Gull Lake, June 8-28, 1929 (E. H. Strickland); 1 ♀, Chin, May 30, 1923 (Walter Carter). NORTHWEST TERR.: 1 ♀, McLeod, June 30, 1902. In the collections of the University of Alberta, the Academy of Natural Sciences of Philadelphia, the U. S. National Museum, the Canadian National Museum, the Illinois State Natural History Survey, and the author.

This species is the only one of its general color known to have a rufous clypeus. In the final analysis, however, the saw is the distinguishing character. It is most apt to be confused with *collaris icterus*, many specimens of which it resembles in the shape of the sheath, but it is easily separated from it and other members of the *bicolor* group by the saw, and from the darker winged forms by the light wings.

Dolerus clypealis var. *nigrilabris* new variety

Female.—Structurally identical with the typical form of *clypealis*, differing in color in having the clypeus black, and both the anterior part of the lateral lobes and the mesoscutum black.

Holotype.—♀, Waterton Lakes, Alberta, Canada, July 12, 1923 (J. McDunnough). Deposited in the Canadian National Museum, Ottawa, Can.

Paratypes.—2 ♀ ♀, Cheboygan, Cheboygan County, Michigan, May 23, 1923 (S. Moore). In the collections of the University of Michigan and the Illinois State Natural History Survey.

Distinguished from *collaris*, *piercei*, *neoagcistus*, etc., by its narrow, pointed sheath and the saw.

Dolerus nortoni new species

Female.—Size small, length 7 mm. Head black; rest of body mostly yellow-rufous, except the following parts which are black: mesonotum except anterior lobe, usually anterior half of lateral lobes, posterior portion of lateral lobes and metanotum except basal plates, pectus and ventral portion of meso-episternum, legs and sheath. Tegulae pale. Wings uniformly clouded with deep brownish-black. Some specimens have the tip of the last tergum and the posterior margin of the abdominal segments lightly washed with black.

Head reticular-rugose; eyes prominent; postocular area contracted behind eye, subequal to length of eye seen from above, with a transverse

diagonal ridge, lateral margin without a carina; posterior margin of head circularly emarginate; vertical furrows deep and wedge-shaped, reaching two-thirds of distance to posterior margin; ocelli slightly closer to posterior margin than to each other, sometimes equidistant; postocellar area twice as wide as long, not raised above postocular area; third segment of antennae subequal to or only very slightly longer than fourth, the remainder gradually diminishing in length; the third segment only slightly constricted above base, the fourth almost columnar. Mesonotum shagreened, dull; anterior lobe flatly convex, disk punctured fairly strongly, sides quite roughly; lateral lobes finely punctuate in centre, sparsely with larger punctures on meson; post-tergite obtusely triangular, sharply striate, with a ridge-like median carina; meso-episternum reticulate with large, uniform punctures; pectus densely shagreened, extremely sparsely punctate; tarsal claws with a very small tooth. Sheath (Figure 26) not forming a distinct scopa, the ventral margin pod-like, narrowly pointed, dorsal margin straight, lower margin curved with a suggestion of a shoulder; five or six setae on each side very much longer than the rest, the setae not directed strongly laterad; cerci attaining about half of dorsal length of sheath; saw (Figure 51) similar in shape to that of *collaris* (Figure 50); alae very narrow, alar spur small, situated midway on annulus; ventral spines pronounced, nearly as long as spur; spurette small and finger-like, not coalescing with ventral margin; lobes fourteen in number, each with two to three teeth, the first one or two straight, the last one remote, finger-like and curved basad; lance with about fourteen annuli, the segments scalloped towards tip.

Male.—Length 6.5 mm. Color entirely black. Wings evenly gray infusate.

Structure similar to female. Punctuation throughout slightly finer. Antennae slightly bi-laterally compressed, more hairy ("prickly") than in *collaris*; hypopygium with more converging sides than *collaris*, much as in *versa*, with the posterior margin slightly rounded. Genitalia as for group.

Holotype.—♀, Muncie, Illinois, April 3, 1916. Deposited in the collection of the Illinois State Natural History Survey, Urbana, Ill.

Allotype.—♂, Urbana, Cottonwoods, Illinois, April 6, 1915 (T. H. Frison). Deposited with the holotype.

Paratypes.—ILLINOIS: 10♂♂, 12♀♀, Urbana, Apr. 3 to 6, 1915 (T. H. Frison); 4♂♂, 6♀♀, Normal, Aug. 18, 1879 (23); 1♀, Urbana, Apr. 23, 1928 (H. H. Ross); 1♀, Urbana, Apr. 16, 1914; 1♀, Urbana, Apr. 16, 1914, feeding on sap of maples; 2♀♀, Muncie, Apr. 3, 1916; 1♀, Little Wabash R., Carmi, Apr. 15, 1914; 1♂, 4♀♀, Urbana, Apr. 4, 1908. MARYLAND: 1♀, Plummer's Id., April 7, 1915 (R. C. Shannon) MASSACHUSETTS: 1♀, Wollaston, July, 1895 (Sprague). MICHIGAN: 4♂♂, 5♀♀, Ann Arbor, Apr. 3, 1921 (T. H. Hubbell); 1♀, Oakland

County, Apr. 23, 1922 (S. Moore); 1 ♀, Ann Arbor, May 6, 1893. NEW YORK: 6 ♀ ♀, Ithaca, Apr. 12 to 26, 1890 to 1913; 1 ♀, Ithaca. ONTARIO: 1 ♀, Ottawa, Apr. 28, 1900. Deposited in a large number of collections.

Easily separated from most specimens of other species of the same color by its small size and the absence of a scopa. In some cases, however, specimens of *nortoni* possess a suggestion of a scopa, in which case it is necessary to exert the saw, which is distinctly characterized by the finger-like teeth of the ventral lobes.

Dolerus nortoni var. *nigritella* new variety

Female.—Size 7 mm. Head black, thorax black with the prothorax, anterior lobe and tegulae rufous, abdomen black. Wings brownish-black as in the typical form. Structurally identical with the typical *nortoni*.

Holotype.—♀, Ithaca, New York, April 28, 1897. In the collection of Cornell University, Ithaca, N. Y.

Known only from the type. Distinguished from *collaris* and *bicolor lesticus*, with which it might be confused, by its small size, lack of a scopa at the apex of the sheath, and the finger-like projections on the ventral lobes of the saw.

Dolerus collaris Say

Dolerus collaris Say, West. Quart. Rep. Cincinnati, Vol. II, 1823, p. 720; Leconte, Writ. Thomas Say Entom., Vol. II, 1859, p. 163; Norton, Proc. Boston Soc. Nat. Hist., Vol. VIII, 1861, p. 152; Norton, Trans. Amer. Ent. Soc., Vol. I, 1867, p. 236; Provancher, Nat. Canad., Vol. X, 1878, p. 71; Provancher, Faun. Ent. Can., Hymen., 1883, p. 197; Riley and Marlatt, Insect Life, Vol. IV, 1891, p. 173; Dalla Torre, Cat. Hymen., Vol. I, 1894, p. 4; MacGillivray, Bull. 22, Conn. Geol. Nat. Hist. Surv., 1916, p. 73.

Female.—Length 7 to 10 mm. Color entirely black, with the prothorax, tegulae, anterior lobe, and paraptera, rufous. Wings uniformly light brown infusate.

Structure, except genitalia, almost identical with *clypealis*, with the following differences, due in most cases to individual variation: postocular area either rotund or shrunken behind eye; mesonotum either not at all, slightly or almost entirely dull and shagreened; pectus densely or lightly shagreened; tarsal claws with a small tooth, similar to *clypealis*.

Sheath as in Figures 27 and 28; wide, but not very thick, scopa wider than in *clypealis*, the ventro-caudal margin more convex; the series of long setae very numerous, projecting almost directly caudad; cerci almost attaining tip of sheath. Saw ovate-ellipsoid; lance with about 18 segments, dorsal margin only finely serrate; lancet with about 16 segments, ventral margin convex, lobes not so notch-like as in *clypealis*, annuli distinct, with short, sparse spines, spurettes small but distinct; no other lateral armature.

Male.—Length 6 to 7 mm. Color entirely black. Wings uniform light brown infusate.

Punctuation of head as in female; postocular area subequal to or slightly longer than eye, seen from above, with a pronounced transverse ridge; third antennal segment a very little longer than fourth, fourth and fifth subequal, the remainder subequal but shorter than fourth, these proportions subject to slight variation; flagellum columnar, slightly bi-laterally compressed, especially at base. Halves of anterior lobe very convex, subglobose; punctuation of mesonotum as in female; pleurae finely, granularly punctate, pectus almost impunctate, entirely or mostly shagreened. Sternites three to six usually four times wider than long, taking curved width; ninth tergite minute, merely a narrow disk visible; hypopygium short, sides of apex almost straight, converging, apex truncate. Genitalia as for group.

Typic locality.—Missouri.

Neotype.—♀, Ames, Iowa, April 21, 1896. Deposited in the collection of the Illinois State Natural History Survey, Urbana, Ill.

Allotype.—♂, Sherman, Illinois, April 3, 1930 (Frison and Ross). Taken in copulation with female. Deposited with neotype.

Distribution.—COLORADO: 1 ♀, Westcliff; 1 ♀, Ft. Collins, Oct., 1900; 1 ♀, Col. CONNECTICUT: 1 ♀, Hartford; 1 ♀, Conn. IOWA: 2 ♀ ♀, Ames, April; 1 ♂, 2 ♀ ♀, Ames, Apr. and May, 1926 (G. Hendrickson). MAINE: 3 ♀ ♀, Orono, April and May. MASSACHUSETTS: 1 ♀, Wellesley, April; 1 ♀, Mass., 1 ♀, Amherst, May 6, 1918. ILLINOIS: 1 ♀, Mahomet, Apr. 3, 1929 (Frison and Park); 1 ♀, Normal, Apr. 18, 1879; many ♂♂, ♀ ♀, Sherman, Apr. 3, 3 ♀ ♀, Seymour, Apr. 10 and 1 ♀, Palos Park, Apr. 24, 1930 (Frison and Ross). MICHIGAN: 4 ♀ ♀, Washtenaw County, April, 1919 to 1921 (T. H. Hubbell). MINNESOTA: 1 ♀, Ft. Snelling, Jn. 6, 1922, flood plain woods (A. A. Nichol). MONTANA: 9 ♂♂, 14 ♀ ♀, Mon. NEBRASKA: 9 ♀ ♀, Lincoln, Holt County and West Point, April (Bruner, Dawson and Gabie). NEW JERSEY: 1 ♀, Manumuskin, May 2, 1909. NEW YORK: 1 ♀, Karner, Apr. 13, 1903; Clinton Hts., Apr. 9, 1903; 1 ♀, Ithaca, Apr. 18, 1896 (On Equisetum) 1 ♀, Fulton, 1 ♀, Ithaca, Apr. 26, 1896. PENNSYLVANIA: 1 ♀, Philadelphia, Apr. 14, 1897; 1 ♀, Castle Rock, Apr. 16, 1911. SOUTH DAKOTA: 2 ♀ ♀, S. D. ALBERTA: 2 ♀ ♀, Edmonton, Apr. 2, 1924 (O. Bryant). MANITOBA: 3 ♂♂, 3 ♀ ♀, Birtle, Apr. 24 to May 11 (R. D. Bird); 3 ♂♂, 2 ♀ ♀, Aweme, Apr. 24 to May 7 (E. and N. Criddle); 1 ♀, Winnipeg, Apr. 30, 1915 (J. B. Wallis). SASKATCHEWAN: 5 ♀ ♀, Oxbow.

This species is easily confused with *bicolor lesticus* from which it can usually be separated by the narrowed scopa of the sheath. The only safe criterion, however, is the shape of the saw.

The female varies in color from being entirely black to the extreme yellowish-rufous condition described in *collaris icterus*. The genitalia of the females remain constant throughout the series, and the males apparently are always black. From this series only four phases have been given varietal names. It would be possible to assign many more to intermediate stages between them but it seems too hair-splitting to do so. These remarks are also true of *bicolor*.

Some authors have considered a British species described by Donovan (1808) as *Tenthredo collaris* to belong to the genus *Dolerus*. Stephens (1829), Dalla Torre (1894) and Konow (1905) all express this view. If this were true, Say's name *collaris* would be preoccupied, and a new name for it would have to be chosen. An examination of the original description of *Tenthredo collaris* Donovan shows that it possesses three closed submarginal cells, which excludes it from *Dolerus*. A careful comparison suggests very strongly that Donovan's species is *Mesoneura opaca* (Fabricius), with which it agrees in wing venation and color, and which synonymy Donovan himself suggests in the original description of *collaris*. This treatment allows Say's *collaris* to stand undisputed in the genus *Dolerus*.

Dolerus collaris var. *erebus* new variety

Female.—Structurally similar to the typical *collaris*. Differs in color in being entirely black, or with only faint spots of reddish on the median or ventro-lateral portions of the collar.

Holotype.—♀, Sherman, Illinois, April 3, 1930 (Frison and Ross). In the collection of the Illinois State Natural History Survey, Urbana, Ill.

Paratypes.—ILLINOIS: 1 ♀, Algonquin, Apr. 26, 1894; 1 ♀, Leroy, Apr. 3, 1907 (Kelly) (38589); 1 ♀, Leroy, May 27, 1907 (Kelly) (38556); 1 ♀, Havana, sand ridges, Jn. 17, 1894 (Hart) (20212); 4 ♀ ♀, Rantoul, Mar. 23, 1930 (H. H. Ross); and 10 ♀ ♀, Seymour, 54 ♀ ♀, Lincoln and 230 ♀ ♀, Sherman, all collected on Apr. 3, 1930 by Frison and Ross. IOWA: 1 ♀, Ames, Apr. 26, 1926 (G. Hendrickson). MINNESOTA: 1 ♀, Ft. Snelling, Apr. 20, 1922 (A. A. Nichol) NEBRASKA: 1 ♀, West Point, Apr. 18 (L. Bruner). SOUTH DAKOTA: 1 ♀. In the collections of the Illinois State Natural History Survey, the University of Minnesota, the University of Nebraska, the South Dakota State College, and the author.

Distinguished from *bicolor*, *nigrita* and *idahoensis* by the shape of the saw and its lack of lateral armature.

Dolerus collaris var. *maculicollis* (Norton)

Dosytheus maculicollis Norton, Proc. Boston Soc. Nat. Hist., Vol. VIII, 1861, p. 153.

Dolerus maculicollis Norton, Trans. Amer. Ent. Soc., Vol. I, 1867, p. 238; Cresson, Mem. Amer. Ent. Soc., No. 5, 1928, p. 7.

Female.—Similar in size and structure to the typical form. Differs in color as follows: head black, thorax rufous with lateral lobes (except a posterior rufous spot), metanotum, including more or less of basal plates, pectus, more or less of lower portions of pleurae, and legs, black. Abdomen with venter black, and sides and most of tergum rufous. Wings brown infusate.

Holotype.—♀, Brooklyn, New York. In the collection of the Philadelphia Academy of Natural Sciences, Philadelphia, Pa.

Distribution.—COLORADO: 2 ♀ ♀, Col. MONTANA: 33 ♀ ♀, Mon. WISCONSIN: 1 ♀, Cranmoor, Apr. 19, 1908. ALBERTA: 1 ♀, Calgary, Apr. 21, 1912 (N. Criddle). MANITOBA: 1 ♀, Aweme, May 10, 1912 (N. Criddle); 1 ♀, Birtle, May 15, 1928 (R. D. Bird). QUEBEC: 1 ♀, Opasatika, Jn. 1 (J. N. Knull). SASKATCHEWAN: 1 ♀, Ogema, Jn. 16, 1916 (N. Criddle); 3 ♀ ♀, Oxbow, Jn. 11, 1907 (F. K. Knab).

Dolerus collaris var. *icterus* MacGillivray

Dolerus icterus MacGillivray, Can. Ent., Vol. XL, No. 4, April, 1908, p. 127; MacGillivray, Bull. 22, Conn. Geol. Nat. Hist. Surv., 1916, p. 71; Frison, Bull. Ill. Nat. Hist. Surv., Vol. XVI, Art. IV, Feb., 1927, p. 241.

Female.—Similar in size and structure to the typical form, differing as follows: head black; thorax rufous with lateral lobes, pectus and legs black; abdomen entirely rufous except sheath, which is black. Wings brown infusate.

Holotype.—♀, Saranac Inn., New York, June 26, 1900 (J. G. Needham). In the MacGillivray Collection, University of Illinois, Urbana, Ill.

Distribution.—COLORADO: 1 ♀, Col. KANSAS: 1 ♀, Douglas County (Beamer). MASSACHUSETTS: 1 ♀, Amherst, May 21, 1904. MINNESOTA: 1 ♀, Hennepin County, June; 1 ♀, Ramsey County, May 9, 1920; 1 ♀, Newport, May 12, 1922 (C. E. Mickel); 1 ♀, Fort Snelling, Apr. 29, 1922, in low prairie grass (A. A. Nichol). NEBRASKA: 1 ♀, Holt County, 6 ♀ ♀, Lincoln, Apr. 11, 1908 (Gable and Dawson). NEW JERSEY: 1 ♀, Ramsey, May 4, 1917. NEW YORK: 1 ♀, Nassau, May 3, 1914; 1 ♀, Ithaca, Apr. 16, 1897. WISCONSIN: 1 ♀, Cranmoor, Jn. 15, 1908 (C. B. Hardenberg). BRITISH COLUMBIA: 1 ♀, Prince Rupert, Apr. 23, 1923 (W. B. Anderson). ONTARIO: 1 ♀, Ottawa, May 5, 1923 (C. H. Curran). QUEBEC: 1 ♀, Levis (T. W. Fyles); 1 ♀, Brome County, Jly. 25, 1916 (A. F. Winn). SASKATCHEWAN: 4 ♀ ♀, Oxbow, Jn. 17, 1907 (F. K. Knab).

These last two color phases are most likely to be confused with *clypealis nigrilabris* and *bicolor*, from which they may be told by the regular and simple condition of the saw.

Dolerus neoagcistus MacGillivray

Dolerus neoagcistus MacGillivray, Bull. Brooklyn Ent. Soc., Vol. XVIII, No. 2, April, 1923, p. 55; Frison, Bull. Ill. Nat. Hist. Surv., Vol. XVI, Art. IV, Feb., 1927, p. 242.

Dolerus neostugnus MacGillivray, Bull. Brooklyn Ent. Soc., Vol. XVIII, No. 2, April, 1923, p. 55; Frison, Bull. Ill. Nat. Hist. Surv., Vol. XVI, Art. IV, Feb., 1927, p. 242. *New synonymy*.

Female.—Length 6 to 9 mm. Head black; remainder of body rufous except the following parts which are black: lateral lobes, meso-scutum, metanotum except basal plates, pectus, legs and sheath. Wings uniformly brown infusate.

Structure, except genitalia, almost identical with *collaris*, with the following slight differences: head always narrower behind eyes; postocellar area slightly raised above level of postocular area, very slightly wider than in *collaris*; anterior lobe flatter, not so strongly convex; tooth of tarsal claws small.

Sheath (Figure 30) with a wide, diamond-shaped scopa, very truncate, margins sharply defined, oblique from lateral view; cerci attaining tip of sheath. Saw as in Figure 52, lance similar to Figure 55; lancet with distinct alae and alar spurs, small in size, situated distant from ventral margin; spurettes well developed, separate only on the four or five apical segments, then gradually fusing with the lobes, appearing at the base as another tooth of the lobe; lobes with from two to five teeth.

Male.—Not yet definitely associated, but undoubtedly a totally black form inseparable as yet from the male of *collaris*, *bicolor*, etc.

Holotype.—♀, Southfields, New York, May 3, 1914 (F. M. Schott). In the MacGillivray Collection, University of Illinois, Urbana, Ill.

Distribution.—Specimens have been examined from the following localities: CONNECTICUT: Hartford. D. C.: Washington. "Del." "Ga." ILLINOIS: Urbana, Dubois, Normal, Danville, Mahomet, Champaign, Centralia, Clinton, Leroy, Bloomington, Chebanse and Thomasboro. INDIANA: Lafayette. KANSAS: Douglas County and Lawrence. MAINE: Orono. MASSACHUSETTS: Cab. John Br., West Springfield, Arlington and Taunton. MICHIGAN: Livingston County. "Min." MISSISSIPPI: Ag. Coll. MISSOURI: St. Louis and Mexico. NEBRASKA: Lincoln. NEW JERSEY: Westville. NEW YORK: Van Cortlandt, New York City, Ithaca, Poughkeepsie, Staten Island, Albany, Normanskill and Sea Cliff. OHIO: Columbus. PENNSYLVANIA: Castle Rock, Edge Hill, Tinicum Island and Ashbourne. VIRGINIA: Roslyn, Great Falls and Falls Church. ONTARIO: Ottawa and Jordan.

Under the 1929 conditions at Urbana, Ill., this species was taken in its greatest abundance towards the end of March when *unicolor* was also at its height, and was taken best in areas of dry grassland, the females of *neoagcistus* coming to the flowering trees at the edge of the meadows. It was also taken intermittently throughout the early spring season at the other habitats studied, but never in abundance. All the records from other localities have been taken in March, April and May, mostly during the latter part of March and the early part of April.

This species is most closely related to *collaris icterus* and *bicolor*, from which it can only be distinguished by the teeth of the saw and the shape of the lateral armature. In a large series the small tarsal claw and the more or less angular lateral edges of the sheath will serve to distinguish it from others of its color, but these characters do not always hold good. The saw is the only reliable character.

Dolerus bicolor (Beauvois)

Tenthredo bicolor Beauvois, Insect. Afr. et Amer., 1805, p. 96.

Dolerus bicolor Lepeletier, Monogr. Tenthred., 1823, p. 122; Norton, Trans. Amer. Ent. Soc., Vol. I, 1867, p. 238; Provancher, Nat. Canad., Vol. X, 1878, p. 72; Provancher, Faun. Ent. Canad., Hymen., 1883, p. 198; Forbes, 14th. Rep. State Ent. f. 1884, 1885, p. 100; Packard, Rep. U. S. Ent. Commiss., No. V, 1890, p. 588; Dalla Torre, Cat. Hymen., Vol. I, 1894, p. 3; MacGillivray, Bull. 22, Conn. Geol. Nat. Hist. Surv., 1916, p. 72.

Dosytheus bicolor Norton, Proc. Boston Soc. Nat. Hist., Vol. VIII, 1861, p. 153.

Female.—Length 7 to 9 mm. Head black; thorax rufous with the following parts black: lateral lobes, sometimes scutum and metanotum in part, pectus and legs; abdomen rufous except sheath. Wings uniformly brown infusate.

Structure, except genitalia, similar to and practically indistinguishable from *collaris*, differing only in having the punctures on the anterior lobe a trifle coarser.

Sheath as in Figures 29 and 31; margins often bevelled and rounded, scopa quite wide, limits more indistinct than in *neoagcistus*, sheath appearing more tube-like, narrower in side-view than *collaris*, with the dorsal margin more or less convex. Saw as in Figure 53, the alae and spurs wider and larger than in *neoagcistus*, closer to the ventral margin, the spurettes more completely fused with the lobes, which are usually less distinctly toothed.

Male.—What are tentatively considered as the males of this species, using coincidental collecting data as criteria of association, are inseparable, either by color or structure, from the males of *collaris*, etc.

Typic Locality.—"Etats-Unis d'Amerique."

Neotype.—♀, Riverton, New Jersey, May 1, 1898. In the MacGillivray Collection, University of Illinois, Urbana, Ill.

Distribution.—CONNECTICUT: 1 ♀, Lyme, May 6 (Greene). KANSAS: 1 ♀, Lawrence, Apr. 24, 1923 (W. G. Garlick). MICHIGAN: 1 ♀, Cavanah Lake, May 24, 1919 (T. H. Hubbell); 1 ♀, Battle Creek. NEBRASKA: 3 ♀ ♀, Holt County, Apr. 26, 1909 (L. Bruner). NEW YORK: 1 ♀, Nassau, May 16, 1906; 1 ♀, Poestenkill, May 6, 1927, 1 ♀, Stephentown, Apr. 3, 1927; 1 ♀, Ithaca, Apr. 26, 1896. VIRGINIA: 1 ♀, Vienna, Apr. 25, 1911 (R. A. Cushman). ILLINOIS: 2 ♀ ♀, "Ill.," April; 1 ♀, DeKalb, May 13, 1930 (Frison and Ross).

This species can be separated from others of the same color, such as

collaris, *neoagcistus* and *clypealis nigrilabris*, only on the basis of the saw, in particular the long and fairly wide alae.

Dolerus bicolor var. *lesticus* MacGillivray

Dolerus lesticus MacGillivray, Can. Ent., Vol. XLVI, No. 3, Mar., 1914, p. 105; Frison, Bull. Ill. Nat. Hist. Surv., Vol. XVI, Art. IV, Feb., 1927, p. 241.

Dolerus graenicheri MacGillivray, Can. Ent., Vol. XLVI, No. 3, Mar., 1914, p. 107; Frison, Bull. Ill. Nat. Hist. Surv., Vol. XVI, Art. IV, Feb., 1927, p. 241. *New synonymy*.

Female.—In size and structure identical with the typical form of the species. Differs only in color, being entirely black except for the collar and anterior lobe, which are rufous.

Type.—♀, Durham, New Hampshire, 2435 (Weed and Fiske). Hampton, New Hampshire, May 1, 1904 (S. A. Shaw). In the MacGillivray Collection, University of Illinois, Urbana, Ill.

Lectoallotype.—♂, same data, (Frison, 1927).

Distribution.—MASSACHUSETTS: 1 ♀, Holyoke, Apr. 12, 1903; 1 ♀, Wellesley, April. MICHIGAN: 1 ♀, Ann Arbor, Apr. 11, 1917. MISSOURI: 1 ♀, C. Mo., (C. V. Riley). NEBRASKA: 1 ♀, Holt County; 4 ♀ ♀, West Pt., April 14 (L. Bruner). NEW YORK: 1 ♀, Ithaca, May. WISCONSIN: 2 ♀ ♀, Cranmoor, May 2, 1908. MANITOBA: 1 ♀, Birtle, May 11, 1928 (R. D. Bird). ONTARIO: 2 ♀ ♀, Ottawa, Apr. 27, 1921 (J. McDunnough); 1 ♀, Ottawa, Jly. 14. QUEBEC: 3 ♀ ♀, Montreal, Apr. 16 to May 14, (J. W. Buckle).

Separated from *collaris* by the shape of the alae, and from *nortoni nigritella* by the sheath and saw.

Dolerus bicolor var. *nigrita* new variety

Female.—Similar in size and structure to the typical *bicolor*. Differs in color in having the body entirely black, except sometimes a small portion of the collar which may be reddish.

Holotype.—♀, Algonquin, Illinois (Nason). Deposited in the collection of the Illinois State Natural History Survey, Urbana, Ill.

Paratypes.—1 ♀, same data as holotype; 1 ♀, Ames, Iowa, April 26, 1926 (G. Hendrickson); 1 ♀, Gray's Lake, Illinois, April 23, 1930 (Frison and Ross). In the collections of the Illinois State Natural History Survey and the author.

Most similar to *collaris erebus* and *idahoensis*, but is readily separated by the shape of the saw.

Dolerus agcistus MacGillivray

Dolerus agcistus MacGillivray, Can. Ent., Vol. XL, No. 4, April, 1908, p. 129; MacGillivray, Bull. 22, Conn. Geol. Nat. Hist. Surv., 1916, p. 73; Frison, Bull. Ill. Nat. Hist. Surv., Vol. XVI, Art. IV, Feb., 1927, p. 240.

Female.—Length 8 to 10 mm. Head black; thorax rufous except the following parts which are usually black; lateral lobes, scutum, metanotum except basal plates, pectus and legs, sometimes also a median triangular area on anterior lobe, and sometimes all the pleurae except the sutures which are always rufous; abdomen rufous except sheath which is black, and cerci which are sometimes black. Scutum apparently always black. Wings light brown infusate, lighter than in *collaris* or *bicolor*.

Structure, except genitalia, as in *collaris*. Postocular area always robust; pectus sometimes shining, not shagreened. Some of tarsal claws with a large tooth, sometimes almost as large as outer hook (Figure 13.)

Sheath large, truncate and barrel-like (Figure 32), scopa wide, margins usually rounded; cerci attaining apex of sheath; lance as in Figure 56, very little serrate; lancet as in Figure 54; alae very greatly developed, especially in the middle region, alar spurs blunt; spurettes also large, blunt and distinct; lobes coarsely toothed three or four times.

Male.—Length 7 to 8.5 mm. Color entirely black, wings very lightly brown infusate.

Structure identical with the males of *collaris* and *bicolor*; usually with the pectus shining, not shagreened and with the hind femora more coarsely punctate. Genitalia typical for group.

Type.—♀, Lake Forest, Illinois (J. G. Needham). In the MacGillivray Collection, University of Illinois, Urbana, Ill.

Allotype.—♂, Seymour, Illinois, April 14, 1929 (Park and Ross). In the collection of the Illinois State Natural History Survey, Urbana, Ill. Present designation.

Distribution.—COLORADO: 4 ♀ ♀, Col. CONNECTICUT: Millford. ILLINOIS: Lake Forest, Algonquin, Summit, Champaign, Onarga, Paxton, Rantoul, Ashkum, Ludlow, Thomasboro, Chebanse, Snyder, St. Joseph, Urbana, Woodyard, Seymour, White Heath, Chicago. INDIANA: East Gary. KANSAS: St. Johns, Grove County, Douglas County, Wallace County, Riley County, Manhattan, Lawrence. LONG IS.: 3 ♀ ♀, L. I. MAINE: Orono. MASSACHUSETTS: Cambridge, Chicopee, West Springfield. MICHIGAN: Douglas Lake. MINNESOTA: Wadena. MONTANA: 2 ♀ ♀, Mon. NEBRASKA: Ashland County, Holt County, West Point, Lincoln. NEW JERSEY: Snake Hill. NEW YORK: Utica, Richfield Springs, Lahaway Ocean County, Staten Island, Pike. OHIO: Columbus. VIRGINIA: Potomac Creek. WYOMING: Lander. MANITOBA: Husavick, Winnipeg.

In the 1929 collecting campaign around Urbana, this species was found to be at its greatest abundance in the Equisetum-Carex communities along the railroads (Figure 72) during April, appearing with *aprilis* and *illini* in the first peak of the abundance of members of this genus in this type of habitat. The dates accompanying the other distribution records are of

a more scattered nature, ranging from April to July, mostly April and May.

This species can usually be distinguished from *collaris icterus*, *bicolor* and *neoagcistus* by its larger size, coarser tooth of the tarsal claws, and wide barrel-shaped sheath. Small specimens, however, cannot be separated from these without the exertion of the saw, which is immediately characterized by the wide and spreading alae. The species can be separated from similarly colored specimens of *piercei* by the robust sheath.

Dolerus agcistus var. *maroa* new variety

Female.—Structurally identical with the typical *agcistus*. Differs in color in having more black on the thorax. Head black; thorax black except first parapterum which is rufous; abdomen beyond basal plates rufous with sheath and its basal sclerites black. Wings lightly infusate as in *agcistus*.

Holotype.—♀, Elkhart, Illinois, May 3, 1930 (Frison and Ross). In the collection of the Illinois State Natural History Survey.

Known only from the holotype. This form most resembles *abdominalis*, but differs in having the sclerites at the base of the sheath black, in having the pleurae more finely punctured, and in the more opaque appearance of the head and thorax.

Dolerus distinctus Norton

Dolerus distinctus Norton, Trans. Amer. Ent. Soc., Vol. IV, 1872, p. 82; Cresson, *ibid.*, Vol. VIII, 1880, p. 39; Cresson, Mem. Amer. Ent. Soc., No. 5, 1928, p. 5.

Female.—Length 10 mm. Head black; thorax black, with the prothorax, anterior lobe, metapleurae and sutures of mesopleurae, rufous; abdomen with dorsum rufous except first tergite and apex of other tergites which are black, and venter and sheath which are black. Wings brownish infusate.

Structure identical with *agcistus*, but the scopa of the sheath is distinctly margined (Figure 32) and the spurettes are a little more distinct.

Male.—Unknown, but undoubtedly similar to that of *agcistus*.

Type.—♀, San Francisco, California (H. Edwards). In the collection of the Philadelphia Academy of Natural Sciences, Philadelphia, Pa.

Distribution.—Only one other specimen besides the type has been examined, namely, 1 ♀, Corvallis, Oregon, June 8, 1892.

This species is separated from others of the same color, *collaris maculicollis* and possibly some specimens of *bicolor*, by its large size and wide alae of the saw. It is separated from *atcistus* by the black venter and more distinctly margined sheath. It is quite possible that this species and *agcistus* are merely color phases of the same species, but a series of 130 females taken in the vicinity of Urbana, and another of 23 females taken

at Douglas Lake, Michigan, by C. H. Kennedy, shows no indication of *agcistus* having variants with a black venter, so that the two are kept distinct. Should they prove the same, *agcistus* will become a race or subspecies of *distinctus*.

Dolerus moramus new species

Male.—Length 8 mm. Head black; thorax black with the prothorax, anterior lobe, tegulae, dorsal margin or all of meso-episternum, and all of meso-epimeron, and metapleurae, rufous; abdomen entirely rufous, except cerci which are black. Wings uniformly brownish infusate.

Head densely punctate below vertex; postocular area slightly shorter than eye, seen from above, robust but not extending as far laterad as the eye, the corner rounded, the posterior margin without a carina, shining and with larger but sparser punctures than other parts of head; posterior margin of head evenly concave, but not deeply so; vertical furrows deep and trench-like, separated from posterior margin by a thick wall; post-ocellar area subquadrate, elevated above level of rest of vertex; lateral ocelli equidistant from each other and posterior margin of head; flagellum subcylindrical, columnar, first segment slightly longer than second, rest gradually decreasing in length. Disk of anterior lobe shagreened, sparsely punctate, lateral areas closely but finely punctate; lateral lobes shining, sparsely punctured; post-tergite subtriangular, the apex rounded, the latero-basal portions striate, the remainder usually shining, median carina rounded and indistinct; meso-episternum reticulately, evenly punctured, punctures intermediate in size between *agcistus* and *eurybis*; pectus more or less shagreened, moderately closely punctured; tarsal claws with a small tooth. Hypopygium short and broad, sides of apex very oblique, apical margin truncate. Genitalia as for group.

Female.—Length 9 mm. Head black; thorax rufous except the following parts which are black: lateral lobes, scutum, metanotum, pectus, and legs; abdomen rufous except sheath and cerci which are black. Wings deep brownish-purple infusate shading near apex to lighter brownish.

Structure, including sheath and saw, identical with *agcistus*.

Holotype.—♂, Algonquin, Illinois, May 28, 1909 (Nason). In the collection of the Illinois State Natural History Survey, Urbana, Illinois.

Allotype.—♀, Fox Lake, Illinois, May 15, 1930 (Frison and Ross). Deposited with holotype.

Paratypes.—ILLINOIS: 1♂, Algonquin, May 20, 1909 (Nason). COLORADO: 4♂♂, "Col.," Baker Collection (2181). MINNESOTA: 2♂♂, Hennepin County. NEW YORK: 1♂, Ithaca, April 26, 1896; 1♂, Ithaca, May 16, 1897. In the collections of the Illinois State Natural History Survey, Cornell University, the University of Minnesota, the U. S. National Museum and the author.

The male of this species can be distinguished from all other males of the genus by the color pattern of rufous and black on the mesonotum together with the entirely rufous abdomen. The female is closest to *D. agcistus* from which it can be separated by the darker wings. The association of these two sexes is made largely on conjecture and may prove to be erroneous.

Dolerus idahoensis new species

Female.—Length 7.5 mm. Color entirely black. Wings very faintly brownish infusate.

Structure, except genitalia, identical with *collaris* and *agcistus*, genitalia identical with the latter. Postocular area robust, with a very low transverse ridge, no carina along posterior margin, the median portion of the ridge practically impunctate, and shagreened; postocellar area subquadrate, slightly raised above level of postocular area; third antennal segment much longer than fourth, distinctly narrower in middle. Anterior lobe almost uniformly convex, disk shining, sides densely punctured; lateral lobes shining, sparsely punctate; post-tergite subtriangular, distinctly striate, with a sharp median carina; meso-episternum more or less smoothly reticulately punctate; pectus fairly densely punctate, shining.

Sheath with edges of scopa very rounded, stout as in *agcistus* (Figure 32), saw as for *agcistus* (Figures 54 and 56).

Male.—Unknown.

Holotype.—♀, Moscow, Idaho, May 6, 1912 (J. M. Aldrich). Deposited in the collection of the Illinois State Natural History Survey, Urbana, Ill.

Known only from the holotype. Distinguished from *collaris erebus* and *bicolor nigrita* by the saw, and from other species in the group by its black color. It is considered as a distinct species, rather than a color variety of *distinctus*, with which it agrees structurally, because of its small size and the small tooth of the tarsal claws, and because no intergrade has been found between *idahoensis* and *distinctus* or *agcistus*.

Dolerus interjectus new species

Female.—Length 6 to 7 mm. Body black, except abdomen which is yellowish-rufous, with the two apical segments entirely or clouded with black. Wings hyaline.

In structure very similar to *collaris*. Head and thorax with white pubescence denser than any other member of group. Head densely punctate except centre of postocular area which is sparsely punctate and shagreened; postocular area as long as eye, seen from above, robust, with a

transverse ridge; scarcely narrowed behind, corners rounded, posterior area slightly wider than long, coarsely punctate, raised a little above post-ocular area; posterior margin of head evenly concave; lateral ocelli equidistant from each other and posterior margin of head; third segment of antennae distinctly longer than fourth, distinctly constricted just before middle, remaining segments columnar and more or less equal. Disk of anterior lobe shining, sparsely punctured, lateral areas rough, very densely punctured; lateral lobes shining, with sparse, moderately large punctures; post-tergite triangular, apex pointed, distinctly striate, with a sharp median ridge; meso-episternum smoothly but deeply reticulately punctured, the walls of the punctures rounded and smooth; pectus shining, sometimes indistinctly shagreened, finely and sparsely punctured, the diagonal row distinct; tarsal claws with a minute inner tooth. Sheath short and stout (Figure 31), scopa wide and very much rounded; setae abundant, with the usual number of long ones, pointing more caudad than laterad; cerci attaining apex of sheath. Saw as for *agcistus* (Figure 54).

Male.—Length 6.5 to 7 mm. Color entirely black except for the three or four basal segments of the abdomen which are rufous. Wings hyaline.

Structure similar to female, with the following differences: antennae columnar, third segment slightly longer than fourth, not constricted, the remaining segments gradually decreasing in length and thickness; pectus usually more or less shagreened; hypopygium and genitalia as for group.

Holotype.—♀, Potlatch, Idaho, June 20, 1907 (J. M. Aldrich). Deposited in the collection of the Illinois State Natural History Survey, Urbana, Ill.

Allotype.—♂, same data as holotype, and deposited with it.

Paratypes.—CALIFORNIA: 3♂♂, Redwood Cañon, Marin County, May 17, 1908. IDAHO: 4♂♂, 1♀, same data as holotype; 1♀, Moscow, June 18, 1895. WASHINGTON: 1♀, Pullman, May 20, 1901; 1♀, Pullman, April; 1♀, Pullman, May 23, 1909 (W. M. Mann); 1♀, Pullman, May 30, 1908. In the collections of the University of Idaho, the State College of Washington, the Illinois State Natural History Survey, the Academy of Natural Sciences of Philadelphia and the author.

This species is readily distinguished from all other species of the *bicolor* group by having the metapleurae black and the abdomen entirely rufous except sometimes the apex. It differs from *abdominalis*, which it most closely resembles in color, by its small size and more finely punctured pleurae. It differs from the members of the *similis* group which it resembles in color by its finely and evenly punctate pleurae, its distinct sheath, typical of the *bicolor* group, and its saw. The male can be distinguished from *nativus* by its smaller size, lighter wings, even punctuation of the postocular area, and more truncate hypopygium. From other members of the *bicolor* group it may be separated by its color, and from the *similis* group

by its small size and very fine and even punctuation of the meso-episternum.

Dolerus eurybis new species

Female.—Length 8 to 9 mm. Body yellow-orange, with the following parts black: head, lateral lobes, tegulae, pectus, legs and base of sheath. Front wings deeply chocolate-infusate basad of stigma, apical half hyaline; hind wings similarly infusate with apical fourth hyaline.

Head below vertex reticulate, vertex more or less shining; postocular area shorter than eye, seen from above, rarely robust, usually narrowed behind eye, corner nearly angular, posterior margin with a slight carina, a broad elevation extending from base of vertical furrow to behind eye, the elevation shining and smooth, sparsely punctate, rarely with a suggestion of shagreening, punctures in the depression behind elevation large; posterior margin of head arcuate, transverse behind postocellar area; the latter slightly wider than long, shining, with sparse punctures, only elevated a little above postocular area; third segment of antennae constricted before middle, distinctly longer than fourth, the remaining segments very gradually decreasing in length. Thorax shining; halves of anterior lobe subcarinate; disk of anterior lobe very minutely punctured; lateral areas more coarsely and densely punctured but nevertheless shining; lateral lobes polished, evenly and minutely punctured; post-tergite triangular, striate, with a sharp median carina; meso-episternum evenly reticulate with large, bowl-like punctures, much larger than in *collaris* or *agcistus*, but not appearing rough; pectus polished, with minute dense punctures, the diagonal row large and distinct; tarsal claw with a very small tooth. Abdomen shining; sheath blunt and barrel-like, with many short black setae at the base of the others, with the characteristic row of long ones; the scopa truncate and wide with rounded sides; cerci projecting beyond sheath; saw as for *agcistus* (Figure 54).

Male.—Length 7 to 8 mm. Head black; thorax black except for the meso-epimeron in part and the metapleurae entirely, which are rufous; abdomen entirely rufous. Wings as in female.

Structure similar to female, with the following differences: third segment of antennae cylindrical, not constricted, longer than fourth, the remainder diminishing in length and width; hypopygium squarely truncate, short; genitalia typical for group.

Holotype.—♀, Cherryfield, Maine, August 8. In the MacGillivray Collection, University of Illinois, Urbana, Ill.

Allotype.—♂, Ottawa, Canada, July 14. In the Canadian National Museum, Ottawa, Canada.

Paratypes.—COLORADO: 1 ♀, Col. (Pergande Collection). MICHIGAN: 1 ♀, "Mich." MINNESOTA: Wadena, Jly 4, 1922 (W. E. Hoff-

man). MANITOBA: 1 ♀, Teulon, Jly 10, 1923 (A. J. Hunter); 1 ♀, Rosebank, Jly. 14, 1924 (J. B. Wallis). QUEBEC: 6 ♀ ♀, Hull, Jly. 28, 1920 (J. McDunnough); 2 ♀ ♀, Hull, Jly. 19, 1914 (J. I. Beaulne); 1 ♀, St. Therese Isl., St. John's County, Jly. 3 (G. Chagnon); 2 ♀ ♀, Rigand, Jly. 10, 1899; 1 ♀, Montreal, Jn. 4, 1899. ONTARIO: 1 ♂, Ottawa, Aug. 14; 1 ♂, 2 ♀ ♀, Harrington Collection. 1 ♀, Peabody Academy. Deposited in the collections of the U. S. National Museum, the Canadian National Museum, the University of Minnesota, the Museum of Comparative Zoology, the Illinois State Natural History Survey and the author.

This beautiful species may be readily distinguished in both sexes by the color of the wings, the like of which has not yet been found in any other species of the genus. In addition, the female may be separated from *agcistus* by the rufous scutellum and from *abdominalis* by the rufous on the mesonotum.

Dolerus abdominalis (Norton)

Dosyltheus abdominalis Norton, Proc. Boston Soc. Nat. Hist., Vol. VIII, 1861, p. 153.

Dolerus abdominalis Norton, Trans. Amer. Ent. Soc., Vol. I, 1867, p. 237; Provancher, Nat. Canad., Vol. X, 1878, p. 71; Provancher, Faun. Entom. Can., Hymen., 1883, p. 197; Dalla Torre, Cat. Hymen., Vol. I, 1894, p. 1; MacGillivray, Bull. 22, Conn. Geol. Nat. Hist. Surv., 1916, p. 74.

Female.—Length 7.5 mm. Head black; thorax black except sutures of meso-epimeron and the metapleurae entirely, which are rufous; abdomen rufous except sheath which is black. Wings evenly lightly or moderately darkly infusate.

Structure almost identical with *eurybis*. Differs as follows: punctures of pleurae very large, but not quite as large; scopa of sheath not so distinct, corners more rounded, halves of anterior lobe more flatly convex.

Male.—Length 6.5 to 7 mm. Color similar to female.

Structure identical with *collaris*, except some specimens which have the pleurae slightly more coarsely punctate. Hypopygium and genitalia as for group.

This antigeny is based upon color only, for no other criteria, not even of association, are available. What are taken as the two sexes of this species differ in the size of the punctures of the pleurae and the shagreening of the pectus, and the two may represent different species.

Typic Locality.—Maine.

Neotype.—♀, Mt. Tom, Massachusetts, May 30, 1896. Deposited in the MacGillivray Collection, University of Illinois, Urbana, Ill.

Distribution.—GEORGIA: 1 ♂, Ga. ILLINOIS: 1 ♀, N. Ill.; 1 ♀, Algonquin, (Nason). KANSAS: 1 ♀, St. John's County, July; 1 ♂, Lawrence, May 5, 1923 (W. G. Garlick). MASSACHUSETTS: 3 ♂ ♂, Longmeadow, May 14, 1905; 2 ♀ ♀, Mass., May 14, 1905; 1 ♀, Amherst, Jn. 2, 1905; 1 ♂, Mass. NEW YORK: 1 ♂, Richfield Springs, May 8, 1887; 1 ♂, Long

Is.; 4♂♂, Ithaca, Apr. 26, 1896. CONNECTICUT: 2♂♂, Hartford, Apr. 29, 1894. PENNSYLVANIA: 1♂, Delaware County, Apr. 22, 1894.

This species may be separated from all other members of the *bicolor* group by its combination of a red abdomen and a black thorax. From the members of the *similis* group with which it might be confused it differs in the sheath and saw, and in having the metapleurae rufous. The male differs from *eurybis* in having the wings uniformly infusate, and the mesopleurae with larger punctures.

SIMILIS GROUP

Posterior margin of postocular area with a distinct carina (except in *elderi*); pectus shining and punctate, often diagonal row of punctures indistinct; pleurae closely punctate; post-tergite mesally carinate, usually striate; sheath without a scopa, setae slender and silky, without a few which stand out conspicuously longer than the rest, as in the *bicolor* group, but with all of them in an evenly graduated series; lancet with highly developed lateral armature; alar spines, alar spur and ventral spines distinct, spurette differentiated at tip, coalescing with ventral margin basally, lobes well set out, dentation much reduced. Male genitalia as in Figure 68, relatively short and wide; praeputium almost truncate at the base, the apices short compared with *sericeus*; gonocardo wide; pedes broad and truncate.

Dolerus elderi Kincaid

Dolerus elderi Kincaid, Proc. Wash. Acad. Sc., Vol. II, Nov. 24, 1900, p. 359, ♂, ♀.

Dolerus cohaesus MacGillivray, Can. Ent., Vol. XL, No. 4, April, 1908, p. 128, ♀; MacGillivray, Bull. 22, Conn. Geol. Nat. Hist. Surv., 1916, p. 72; Frison, Bull. Ill. Nat. Hist. Surv., Vol. XVI, Art. IV, Feb., 1927, p. 240. *New synonymy*.

Dolerus nutricius MacGillivray, Can. Ent., Vol. LV, No. 7, July, 1923, p. 159, ♂; Frison, Bull. Ill. Nat. Hist. Surv., Vol. XVI, Art. IV, Feb., 1927, p. 244. *New synonymy*.

Loderus acriculus MacGillivray, Univ. Ill. Bull., Vol. XX, No. 50, Aug. 13, 1923, p. 20, ♀; Frison, Bull. Ill. Nat. Hist. Surv., Vol. XVI, Art. IV, Feb., 1927, p. 249. *New synonymy*.

Dolerus nyctelius MacGillivray, Jour. N. Y. Ent. Soc., Vol. XXX, No. 4, Dec., 1923, p. 163, ♂; Frison, Bull. Ill. Nat. Hist. Surv., Vol. XVI, Art. IV, Feb., 1927, p. 244. *New synonymy*.

Dolerus nemorosus MacGillivray, Jour. N. Y. Ent. Soc., Vol. XXX, No. 4, Dec., 1923, p. 164, ♀; Frison, Bull. Ill. Nat. Hist. Surv., Vol. XVI, Art. IV, Feb., 1927, p. 242. *New synonymy*.

Female.—Length 5.5 to 6.5 mm. Head and thorax black: legs black except tibiae which may be almost entirely black or yellowish-rufous with the apices black, and the apices of the anterior femora which are also yellowish-rufous; abdomen rufous with the apical three or four segments black. Wings hyaline, veins light brown.

Head finely reticulate except postocellar area and transverse area of postocular area which are shining; postocular area rotund, with a transverse elevation occupying almost its whole extent, the elevation shining

and only sparsely punctate, the posterior margin heavily punctured, with a carina on the mesal half, the length of the postocular area equal to eye, seen from above. Small specimens may have the postocular area obliquely narrowed behind eyes. Posterior margin of head arcuate, transverse behind ocelli; vertical furrows wide and deep, nearly reaching posterior margin; postocellar area slightly wider than long, convex, shining, sparsely punctate, scarcely raised above level of postocular area; ocellar basin scarcely distinct in some specimens, reticulate or partially striate, its lateral wall hardly raised, in others very distinct, striate and with linear, well-defined walls; flagellum of almost equal width throughout, third antennal segment distinctly longer than fourth, very slightly constricted near base, but not so much as in the *bicolor* group, remaining segments almost subequal. Mesonotum shining; meson of anterior lobe with fine punctures, edges of disk with large, sparse punctures, lateral areas with dense reticular punctures; lateral lobes polished, finely punctured; both anterior lobe and lateral lobes very convex; post-tergite triangular, striate, with a tent-like median carina, the surface not being excavate on each side of it; meso-episternum with large, round, equal, well separated punctures, the walls between them polished and smooth; pectus polished, almost impunctate, the diagonal row very faintly impressed; tarsal claws very little curved, with a very fine tooth about two-thirds distance from base. Sheath relatively thin, without a scopa (Figure 40), dorsal margin straight, ventro-caudal margin shouldered, setae fine and silky, longest in middle and gradually decreasing in size on either side; cerci almost attaining apex of sheath. Saw as in Figure 57, long and narrow; lance serrate above; lancet with lobes and spurrites fused, the spurrite appearing as the basal tooth of the lobe; lobes irregularly toothed with none to five teeth; alae narrow, with distinct spines; alar spur present; ventral spines present on remnant of annuli below alar spur.

Male.—Length 5 to 6.5 mm. Color similar to female, except that the tibiae are usually a little darker.

Structure similar to female, with the following differences: antennae thicker, slightly bilaterally compressed, finely and densely setose; hypopygium slightly longer than wide, apex with sides oblique and posterior margin almost truncate. Genitalia as for group.

Type.—♂, Popoff Island, Alaska, July 10, 1899 (T. Kincaid) (Harriman Alaska Expedition). In the U. S. National Museum, Washington, D. C.

Allotype.—♀, Kukak Bay, Alaska, July 4, 1899 (T. Kincaid) (Harriman Alaska Expedition). Deposited with holotype.

Distribution.—COLORADO; 1 ♀, Durango, Jly. 8, 1899; 1 ♂, 2 ♀ ♀, Ute. Cr., 9000 ft. Alt., Jly. 4 to 8 (Bruner and Smith); 5 ♂ ♂, 3 ♀ ♀, Florissant, Jly. 7, 1907; 1 ♂, 2 ♀ ♀, Florissant, Jn. 16, 1907, on *Salix brachycarpae*

(S. A. Rohwer). ILLINOIS: 1♂, 4♀, Chicago, Aug. 7 to 20, 1904; 1♂, 1♀, Ill.; 1♀, Osborn, Aug. 12, 1916 (C. S. Spooner); 3♀, Garden City, 3♂♂, Waukegan, May 14–15, 1930 (Frison and Ross). INDIANA: 1♂, 4♀, Hessville, Jly. 4 to 30, 1906. MICHIGAN: 9♂♂, 3♀, Onekama, Jly. 5, 1915; 2♂♂, 1♀, Douglas Lake, Aug. 1928 (C. H. Kennedy); 1♂, Huron County, May 17, 1922. MONTANA: 3♂♂, 1♀, Gallatin County, 6800 ft. alt., June to July; 1♀, Bozeman, Jly. 21, 1913. NEVADA: 1♂, Nev. NEW JERSEY: 1♂, Gt. Piece Midw., May 30, 1919. NEW YORK: many ♂♂ and ♀♀, Ithaca, McLean, Caroline, Albany, Poughkeepsie, Otto, Slingerlands, Yonkers, Keen Valley (Essex County), from May to August. OREGON: 2♀, Corvallis, May 13, 1917; 1♂, Union County, Jn. 25, 1922; 8♂♂, 8♀, Mt. Hood; 1♀, Hood River. PENNSYLVANIA: 1♂, 1♀, N. E. Pa., Jly. 18, 1916, on *Equisetum* (R. E. Cushman). SOUTH DAKOTA: 1♂, 1♀, Harney Peak, Jly 22, 1924 (H. C. Severin). WASHINGTON: 1♀, Olympia, Aug. 10, 1894 (T. Kincaid). WASHINGTON TERR: 2♀, W. T. BRITISH COLUMBIA: 2♂♂, 3♀, Revelstoke, Jly., 1905 (J. C. Bradley). ONTARIO: ♂♂ and ♀♀, Ottawa, Brockville, Jordan, Vineland, Pelham, Bonville, from July to September. NEWFOUNDLAND: 3♀, Bay of Islands, July to August. QUEBEC: ♂♂ and ♀♀, Montreal, Hull, Almer, St. Hilaire, Montfort, June to August. ALASKA: 1♂, 3♀, Popoff Islands, Jly. 9, 10 and 13, 1899 (T. Kincaid); 1♀, Kukak Bay, Jly 4, 1899 (T. Kincaid).

A widely distributed species, occurring throughout the Rocky Mountain region from Alaska southward, and stretching across the continent to the middle Atlantic coast. In the northern mountainous regions the species has more black on the legs, particularly in the males, and in the eastern portion of its range usually has the ocellar basin less punctate and more striate, but neither of these variations seem constant enough to warrant separate subspecific names. The species is characterized by its small size, the type of punctuation of the pleurae, the very convex and shining anterior and lateral lobes, and the sheath and saw. It may be separated from *interjectus*, with which it may be confused, by its coarse punctuation of the pleurae and slender, thin sheath; and from *yukonensis*, its nearest relation, in the type of punctuation of the pleurae and the more convex, less densely punctate postocular area and more convex thoracic lobes. Small specimens of *similis* will have very dense punctuation on the postocular area and anterior lobe, and a more irregular type of punctuation on the pleurae.

Dolerus elderi var. *auraneus* new variety

Female.—Similar in size and structure to the typical *elderi*. Differs in color, having the abdomen entirely rufous or with the last two segments more or less black. Hind tibiae black, middle and front tibiae black, yellow-infusate on basal third. Wings slightly uniformly dusky.

Male.—Similar to the typical *elderi*, sometimes with the wings dusky.

Holotype.—♀, Boise, Idaho (J. M. Aldrich). In the MacGillivray Collection, University of Illinois, Urbana, Ill.

Allotype.—♂, same data as holotype. In the collection of the Illinois State Natural History Survey, Urbana, Ill.

Paratypes.—IDAHO: 1♂, 6♀, Boise (J. M. Aldrich); 1♂, Moscow, July 1, 1909 (J. M. Aldrich); 1♀, Caldwell, July 9, 1926 (C. Wakeland). UTAH: 1♂, Emigrant Canyon, Wascatch Mts., 7000 ft. alt., July 8, 1911 (J. M. Aldrich). NEW MEXICO: 1♀, Fort Wingate, July 28, 1909 (John Woodgate). Deposited in the collections of the University of Idaho, Illinois State Natural History Survey and the author.

Apparently confined to the southern Rocky Mountain region. Differentiated on the same characters as *elderi*.

Dolerus elderi var. *rubicannus* new variety

Male and female.—In size and structure similar to the typical *elderi*. Differs in having all the femora and tibiae entirely reddish yellow. The males may have the base of the femora infusate.

Holotype.—♀, Milaca, Minnesota, June 21, 1917. Deposited in the collection of the Illinois State Natural History Survey, Urbana, Ill.

Allotype.—♂, St. Cloud, Minnesota, June 21, 1917. Deposited with the holotype.

Paratypes.—MICHIGAN: 1♀, Gogebie County, July 22, 1919 (T. H. Hubbell). MINNESOTA: 1♂, Milaca, Jn. 21, 1917; 1♀, Rock County, Jn. 24, 1910; 1♂, Ashley, Aug. 28, 1911; 1♀, Calhoun, Jn. 12, 1921 (W. E. Hoffman); 1♀, Rv. nr. Henderson, Sibley County, Jly. 17, 1922 (W. E. Hoffman); 1♀ Rochester, Jn. 13, 1922 (C. E. Mickel). MONTANA: 1♂, Mon. NORTH DAKOTA: 1♀, Turtle Mts., Lake Upsilon, Jly. 14 1919 (C. Thompson). WISCONSIN: 2♀♀, Madison, Sept. 1, 1916 (H. K. Harley). ALBERTA: 1♂, Lethbridge, Aug. 12, 1922 (E. H. Stickland). MANITOBA: 2♀♀, Fork River, Jly. 14, 1926 (E. Criddle); 1♀, Treesbank, Jn. 26, 1926 (R. D. Bird); 2♀♀, Birtle, Jn. 14, 1928 (R. D. Bird); 1♂, Birtle, Jn. 26, 1928 (R. D. Bird). In the collections of the University of Michigan, University of Minnesota, U. S. National Museum, Canadian National Museum, University of Alberta, Illinois State Natural History Survey, Dr. R. D. Bird, and the author.

This interesting variety has so far been taken only in and around the Great Plains. It is distinct among the subgenus *Dolerus* in having the femora red.

Dolerus elderi var. *melanus* new variety

Male and female.—Similar in size and structure to the typical *elderi*. Differs in color in being entirely black, except sometimes as indistinct fuscous area on the dorsum or basal lateral margins of the abdomen.

Holotype.—♀, Saldovia, Alaska, July 21, 1899 (T. Kincaid) (Harriman Alaska Expedition). Deposited in the U. S. National Museum, Washington, D. C.

Allotype.—♂, Agassiz, British Columbia, May 8, 1927 (H. H. Ross). Deposited in the Canadian National Museum, Ottawa, Canada.

Paratypes.—1 ♀, Sitka, Alaska, June 16, 1899 (T. Kincaid, Harriman Alaska Expedition); 1 ♂, 3 ♀ ♀, Mt. Hood, Oregon; 3 ♀ ♀, Agassiz, B.C., May 8, 1927 (H. H. Ross); 1 ♀, Agassiz, B.C., July 15, 1926 (R. Glendenning); 1 ♀, Agassiz, B.C., May 27, 1917 (A. E. Cameron); 1 ♂, Friday Harbor, Washington, May 29, 1906 (J. M. Aldrich). Deposited in the collections of the U. S. National Museum, the University of Idaho, the Philadelphia Academy of Sciences, the Illinois State Natural History Survey, the Canadian National Museum and the author.

This is a melanic variety occurring in the more humid regions of the Pacific Coast. It may be distinguished from other black species by its small size, robust and shining postocular area (especially noticeable in larger specimens), type of punctuation of the pleurae, and the convex and shining anterior and lateral lobes.

Dolerus nasutus MacGillivray

Dolerus nasutus MacGillivray, Can. Ent., Vol. LV, No. 3, Mar., 1923, p. 65; Frison, Bull. Ill. Nat. Hist. Surv., Vol. XVI, Art. IV, Feb., 1927, p. 242.

Dolerus nugatorius MacGillivray, Can. Ent., Vol. LV, No. 3, Mar., 1923, p. 66; Frison, Bull. Ill. Nat. Hist. Surv., Vol. XVI, Art. IV, Feb., 1927, p. 243. *New synonymy*.

Dolerus novellus MacGillivray, Can. Ent., Vol. LV, No. 3, Mar., 1923, p. 67; Frison, Bull. Ill. Nat. Hist. Surv., Vol. XVI, Art. IV, Feb., 1927, p. 243. *New synonymy*.

Female.—Length 8 to 10 mm. Color entirely black. Head with the area between ocelli and eyes having a bluish reflection. Wings hyaline.

Body with white pubescence longer than usual. Head rough and reticulate except postocellar area and transverse area of postocular area which are shining and sparsely punctured; postocular area subequal in length to eye, seen from above, distinctly narrowed behind eye, with a transverse ridge which is usually shining, the posterior margin rough and carinate; vertical furrows deep and pit-like, half length of postocellar area; the latter wider than long; lateral ocelli equidistant from each other and posterior margin of head; antennae as in *elderi*. Mesonotum shining; halves of anterior lobe sharply convex; disk with sparse punctures, sides with large punctures, sparser posteriorly; lateral lobes and post-tergite as in *elderi*; meso-episternum with large, crater-like punctures, reticulate; borderline between pleurae and pectus definitely marked, sharp; pectus flat and shining, fairly densely punctured, diagonal row indistinct; tarsal claws with a moderately large tooth. Sheath as in Figure 35, shaped as in *elderi*, with a fine carina along the dorso-lateral angle a trifle removed from the dorsal edge at base, but converging into it at apex, as is also true of

elderi; setae as in *elderi*; cerci attaining one-half to three-quarters length of sheath. Saw almost identical with that of *elderi*, differing only in having more prominent spurettes (Figure 58).

Male.—Similar in size, color and structure to female. Genitalia as for group.

Type.—♀, Corvallis, Oregon (Laura Hill). In the MacGillivray Collection, University of Illinois, Urbana, Ill.

Lectoallotype.—♂, Corvallis, Oregon, April 20, 1908 (Laura Hill). Deposited with the type. (Frison, 1927).

Distribution.—COLORADO: 1 ♀, Veta Pass, June 21. IDAHO: 1 ♀, Kendrick; 1 ♀, Moscow; 1 ♂, Moscow Mt., June 3, 1911. MONTANA: 3 ♀ ♀, Gallatin County, Apr. 5 to June 11, 1904. NEW MEXICO: 3 ♂ ♂, Jemez Springs, May 17 to 31, 1913 (J. Woodgate); 3 ♂ ♂, 1 ♀, Fort Wingate, May 7 to 14, 1908 (J. Woodgate). OREGON: 2 ♂ ♂, 1 ♀, Corvallis, Apr. 20 to June 8; 1 ♀, Forest Grove, May 12, 1918; 1 ♀, Springfield; 1 ♀, Albany. WASHINGTON: 2 ♂ ♂, 3 ♀ ♀, Pullman, May 20 to 31. BRITISH COLUMBIA: 1 ♂, Agassiz, May 22, 1922 (R. Glendenning) 1 ♀, Agassiz, May 27, 1921 (R. Glendenning); 1 ♂, Hazelton, May 18, 192—(W. B. Anderson); 1 ♂, Vancouver; 1 ♂, Vernon, May 2, 1903; 1 ♂, Chilliwack, May 10, 1927. ALBERTA: 1 ♀, Banff, June 5, 1922 (C. B. Garrett).

A rare species, distributed through the middle Pacific slope and the southern Rocky Mountains. This species is often confused with *nicaeus* and *elderi melanus*. From *nicaeus* it may be distinguished in the female by the narrower sheath with the lateral carina almost confluent with the dorsal margin, the saw, the meso-episternum having circular and almost equal punctures, the sharper angle of the pectus and pleurae, and the postocular area being flat and lacking a transverse ridge; in the male by the polished pectus, practically impunctate adjacent to the pleurae, the even and more rugose punctures of the meso-episternum reaching to the very edge of the pectus and forming a marked division between pleurae and pectus, and the more shining lobes of the thorax. Both sexes possess a bluish reflection on the area of the head between the eyes and ocelli, if seen from certain angles and this serves as a very useful guide to the two species after one becomes accustomed to the character. From *elderi melanus* this species may be immediately separated by the contracted and constricted postocular area, and, usually, the larger size. *Nasutus*, also, lacks grooves on the hind tibiae and can be separated from members of the *sericeus* group on the basis of that character.

Dolerus apriloides MacGillivray

Dolerus apriloides MacGillivray, Can. Ent., Vol. XL, No. 4, April, 1908, p. 126; Frison, Bull. Ill. Nat. Hist. Surv., Vol. XVI, Art. IV, Feb., 1927, p. 240.

Female.—Length 10 to 11 mm. Head and thorax black, legs sometimes with front tibiae rufous, abdomen rufous with the last three segments black. Wings tawny infusate, with the basal fifth of the front wing and basal third of the hind wing hyaline.

Body very robust. Head roughly reticulate, except for the mesal portion of the postocular ridge which is shining; head wider behind eyes than through them; postocular area robust, equal to length of eye seen from above, with a transverse ridge, the posterior margin rough and subcarinate; vertical furrows relatively shallow and cuneiform; postocellar area subquadrate; lateral ocelli equidistant from each other and posterior margin of head; median fovea large, saucer-shaped and shining; antennae as in *elderi*. Disk of anterior lobe closely punctured, opaque, lateral areas with large and small punctures, reticulate; the halves gently convex; lateral lobes very closely punctured except small central disk which is almost smooth; post-tergite very stout and thick, triangular and smooth, with low, granular striations, and with a rounded median carina; meso-episternum slightly depressed just above pectus, with very large, more or less irregular rugosities, presenting a rough appearance; pectus well set off from pleurae, very densely punctate except for postero-mesal corners which are shining; hind tibiae more or less distinctly longitudinally grooved, as in the *sericeus* group; tarsal claws with a medium sized tooth. Sheath resembling Figure 35, but shorter, the carina forming a sharp upper and outer angle; cerci almost attaining tip; saw as for *nasutus* (Figure 58).

Male.—Similar in size, color and structure to female, with the hypopygium and genitalia characteristic of the group.

Type.—♀, Ithaca, New York, June 19, 1897. In the MacGillivray Collection, University of Illinois, Urbana, Ill.

Allotype.—♂, Montreal, Canada, June 25, —. (6689). Deposited in the collection of the Illinois State Natural History Survey, Urbana, Ill.

Distribution.—CONNECTICUT: 1♂, Cornwall, May 28, 1920 (Chamberlain). ILLINOIS: 1♀, Fourth Lake, June 16, 1892 (Hart and Shiga); 1♀, Chicago, June 3, 1906 (W. J. Gerhard). INDIANA: 1♀, Hessville, June 18, 1911. MICHIGAN: 1♀, Douglas Lake, July 23, 1924. MINNESOTA: 1♀, Moore Lake, June 25, 1917. MANITOBA: 1♀, Winnipeg, July 10, 1911 (J. B. Wallis).

This is a rare species taken from the central and eastern part of the continent. Because of its large size this species is most likely to be confused with *neoaprilis*, from which it differs in the female in the sheath and saw and in the male by the larger rugosities around the region of the depression of the pectus, which obscure the sharp margin present in *neoaprilis*. From all other species of the same color it differs in the rugose pleurae and robust head.

Dolerus yukonensis Norton

Dolerus similis var. *yukonensis* Norton, Trans. Amer. Ent. Soc., Vol. IV, 1872, p. 141; Dalla Torre, Cat. Hymen., Vol. I, 1894, p. 17; Cresson, Mem. Amer. Ent. Soc., No. 5, 1928, p. 10.

Dolerus nuntius MacGillivray, Can. Ent., Vol. LV, No. 7, July, 1923, p. 158; Frison, Bull. Ill. Nat. Hist. Surv., Vol. XVI, Art. IV, Feb., 1927, p. 244. *New synonymy.*

Dolerus nundinus MacGillivray, Can. Ent., Vol. LV, No. 7, July, 1923, p. 159; Frison, Bull. Ill. Nat. Hist. Surv., Vol. XVI, Art. IV, Feb., 1927, p. 244. *New synonymy.*

Female.—Length 7 to 8 mm. Head and thorax black except bases of tibiae which are more or less rufous; abdomen rufous at base, black at apex, segments 6 to 10 almost entirely black, and the ventral corners of the basal terga black, forming a checkered line on the ventro-lateral aspect. Wings hyaline, barely stained with tawny.

Head evenly, finely reticulate, with at most a small area on postocular area less densely reticulate; eyes prominent, head reduced in width behind eyes; postocular area slightly shorter than length of eye seen from above, with a narrow ridge, not very high, and a posterior carina; vertical furrows small, shallow and elliptical; postocellar area flat, scarcely convex, punctured the same as the head, wider than long, not raised above level of postocular area. Mesonotum densely punctured, lateral areas of anterior lobe with large, rugged punctures; disk and lateral lobes shining but with dense punctures; post-tergite triangular, densely striate, with a sharp median carina; meso-episternum depressed just above pectus, the depression with a rugged, circular posterior carina, the entire area with large, but very shallow, punctures, giving it a rough appearance; pectus shining, very densely punctate, diagonal row distinct; pectus and pleurae merging into each other gently, without a separating ridge; tarsal claws with a small tooth. Genitalia identical with *nasutus* (Figures 35 and 58).

Male.—Length 7 mm. Color and structure similar to female; in some specimens the black is reduced on the ventral corners of the rufous sternites; hypopygium with the apical margin slightly rounded; genitalia as for group.

Lectotype.—♀, Alaska. In the collection of the Philadelphia Academy of Natural Sciences, Philadelphia, Pa.

Distribution.—ALBERTA: 3♂♂, 18♀♀, Banff, June 1 to 26, 1922 (C. B. Garrett); 1♀, Shovel Pass, Jasper Park, July 1, 1915; 1♂, 1♀, Edmonton, June 6, 1917 and May 21, 1915 (F. S. Carr). ALASKA: 1♀, Yakutat, June 21, 1899 (T. Kincaid); 1♀, St. Paul Island, Bering Sea (E. A. Preble) (Summer, 1914).

Confined to the northern Rocky Mountains and Alaska. The female differs from *interjectus*, which it resembles in many particulars, in the saw and sheath, from *elderi* in having the head evenly and finely punctate, and from *similis* in the sheath and saw, its smaller size, more finely punctate

and flatter head, and the lateral black bars on the red basal portion of the venter. The male differs from *interjectus* in the roughness of the pleurae, from *elderi* and *similis* in the same characters as the female.

Dolerus similis (Norton) *sens. lat.*

Considered in its widest sense, this species is remarkably variable in size and color, but very constant in structure, with the exception of the sheath. Two extreme forms of the sheath occur, a very short one, represented by Figures 33 and 37, and a long one represented by Figures 34 and 38. In the central and eastern parts of the continent these two extremes occur in the same series, and in the Illinois collections the extremes and many intermediates were taken many times at the same time and place. In the Rocky Mountain region all large series showed a great constancy of this character, the extremes never yet having been taken together. In addition to this, many series exhibited variations in color, especially of the legs and wings, which were encountered from only the one locality. The punctuation of the head and thorax, the shape of the saw, and the male genitalia were constant throughout the entire series of variations. It suggests that the isolation and habitats of different physiological conditions afforded by the mountainous area have allowed local strains or races of this species to become established, which do not yet seem distinct enough, or far enough along in the scale of evolution, to be considered valid species.

The following key will separate the known varieties and races of *Dolerus similis*:

- Females.....1
- Males.....10
- 1. Wings uniformly infusate, especially at base, sometimes paler at apex.....2
- Wings never infusate at base, sometimes tawny in the middle or towards apex.....6
- 2. Tibiae rufous, hind pair sometimes darker at apex.....*similis* var. *tibialis* Cress.
- Tibiae mostly black.....3
- 3. Thorax mostly black, sometimes clouded with rufous.....4
- Anterior and lateral lobes rufous, anterior lobe sometimes with a median black triangle..5
- 4. Sheath shorter, as in Figure 33, the lateral carina indistinct, the setae longer and more divergent, without a visible shining area between setae and lateral portion of dorsal plates.....*similis* var. *conjectus* Ross
- Sheath longer, as in Figure 34, lateral carina distinct and straight, setae shorter, with a distinct shining area between setae and lateral portion of dorsal plates.....*similis* subsp. *fumatus* Ross
- 5. Length 7.5 to 9.0 mm.; postocular area usually finely punctate, dull; anterior lobe sometimes with a black median triangle which in extreme cases migrates on to the meson of the lateral lobes; abdomen often with the apical segments black, more often entirely rufous; tibiae entirely black.....*similis* subsp. *simulans* Roh.
- Length 9.5 to 10.5 mm.; postocular area shining, sparsely punctate; anterior and lateral lobes and abdomen always entirely rufous; front tibiae sometimes entirely or partly rufous.....*similis* subsp. *nescius* MacG.

6. Both anterior and lateral lobes rufous, anterior lobe sometimes with a black median triangle.....7
- At most anterior lobe and indefinite areas on posterior corners of lateral lobes rufous. .8
7. Tibiae entirely black; anterior lobe sometimes with a black median triangle
.....*similis* subsp. *simulans* Roh.
- Front tibiae mostly rufous, middle tibiae sometimes rufous at base; anterior lobe entirely rufous.....*similis* var. *novicius* MacG.
8. Thorax entirely black, except sometimes fore tibiae at base.....9
- Thorax with at least a great part of prothorax, usually with collar and anterior lobe rufous.....*similis* (Nort.) *sens. st.*
9. Sheath short, as in Figure 33, lateral carina indistinct, without a shining area between the apical area of setae and the lateral portion of dorsal plates.....*similis* var. *nummarius* MacG.
- Sheath longer, as in Figure 34, lateral carina distinct, and with a shining area between the apical area of setae and the lateral portion of dorsal plates.....*similis* subsp. *nordanus* Ross
10. Tibiae rufous, except sometimes hind pair at apex; wings infusate.....*similis* var. *tibialis* Cress.
- Tibiae black, except sometimes front and middle pair at base.....11
11. Wings fairly deeply infusate at base, sometimes paler at apex.....12
- Wings hyaline at base, sometimes infusate in middle or at apex. *similis* (Nort.) *sens. st.*
.....*similis* var. *nummarius* MacG.
.....*similis* subsp. *nordanus* Ross
.....*similis* subsp. *simulans* Roh. in pt.
12. Size large, 9.5 to 10 mm.; transverse ridge of postocular area shining, sparsely punctate.....*similis* subsp. *nescius* MacG.
- Size smaller, 8 to 9 mm.; postocular area usually fairly densely punctate, dull.....*similis* var. *conjectus* Ross.
.....*similis* subsp. *fumatus* Ross
.....*similis* subsp. *simulans* Roh. in pt.

The light winged forms of this species resemble *elderi*, *yukonensis*, *aprilis*, *apriloides* and *neoaprilis* in color. In the female *aprilis* and *neoaprilis* are easily distinguished by the sheath; *apriloides* differs in its rugose pleurae; *elderi* and *yukonensis* differ in the saw, slightly in the sheath, *elderi* in its much smaller size, the robust and shining postocular area, the convex and shining anterior and lateral lobes, and the circular, smooth type of punctuation of the meso-episternum, *yukonensis* in its evenly punctured head, flat and densely punctured postocular area, and evenly confluent pectus and pleurae. The males of *apriloides* and *neoaprilis* can be separated on the basis of the stocky and shining post-tergite, more robust and longer postocular area, rugose and depressed pleurae and longer hypopygium; those of *elderi* by the smaller size, robust and shining postocular area and thoracic lobes, and the type of punctuation of the meso-episternum; and those of *yukonensis* on the flatter and densely punctate postocular area lacking a transverse ridge, and more confluent pectus and pleurae. No satisfactory difference has yet been found between the males of *similis* and *aprilis*.

The dark winged forms are usually distinct by their color and are seldom confused with any other species. The one or two exceptions are noted under the individual forms.

Dolerus similis (Norton) *sens. st.*

Dosytheus similis Norton, Proc. Boston Soc. Nat. Hist., Vol. VIII, 1861, p. 153.

Dolerus similis Norton, Trans. Amer. Ent. Soc., Vol. I, 1867, p. 238; Provancher, Nat. Canad., Vol. X, 1878, p. 72; Provancher, Faun. Ent. Can., Hymen., 1883, p. 198; Dalla Torre, Cat. Hymen., Vol. I, 1894, p. 17; MacGillivray, Bull. 22, Conn. Geol. Nat. Hist. Surv., 1916, p. 74.

Dolerus conjugatus MacGillivray, Can. Ent., Vol. XL, No. 4, April, 1908, p. 128; MacGillivray, Bull. 22, Conn. Geol. Nat. Hist. Surv., 1916, p. 73; Frison, Bull. Ill. Nat. Hist. Surv., Vol. XVI, Art. IV, Feb., 1927, p. 241. *New synonymy.*

Dolerus plesius MacGillivray, Can. Ent., Vol. XL, No. 4, April, 1908, p. 129; MacGillivray, Bull. 22, Conn. Geol. Nat. Hist. Surv., 1916, p. 73; Frison, Bull. Ill. Nat. Hist. Surv., Vol. XVI, Art. IV, Feb., 1927, p. 244. *New synonymy.*

Dolerus inspectus MacGillivray, Can. Ent., Vol. XL, No. 4, April, 1908, p. 128; MacGillivray, Bull. 22, Conn. Geol. Nat. Hist. Surv., 1916, p. 72; Frison, Bull. Ill. Nat. Hist. Surv., Vol. XVI, Art. IV, Feb., 1927, p. 241. *New synonymy.*

Dolerus stugnus MacGillivray, Can. Ent., Vol. XL, No. 4, April, 1908, p. 129; MacGillivray, Bull. 22, Conn. Geol. Nat. Hist. Surv., 1916, p. 74; Frison, Bull. Ill. Nat. Hist. Surv., Vol. XVI, Art. IV, Feb., 1927, p. 244. *New synonymy.*

Dolerus acritus MacGillivray, Can. Ent., Vol. XL, No. 4, April, 1908, p. 130; MacGillivray, Bull. 22, Conn. Geol. Nat. Hist. Surv., 1916, p. 74; Frison, Bull. Ill. Nat. Hist. Surv., Vol. XVI, Art. IV, Feb., 1927, p. 240. *New synonymy.*

Dolerus inspiratus MacGillivray, Can. Ent., Vol. XLVI, No. 3, March, 1914, p. 105; MacGillivray, Bull. 22, Conn. Geol. Nat. Hist. Surv., 1916, p. 72; Frison, Bull. Ill. Nat. Hist. Surv., Vol. XVI, Art. IV, Feb., 1927, p. 241. *New synonymy.*

Dolerus nefastus MacGillivray, Can. Ent., Vol. LV, No. 3, March, 1923, p. 66; Frison, Bull. Ill. Nat. Hist. Surv., Vol. XVI, Art. IV, Feb., 1927, p. 242. *New synonymy.*

Dolerus nummatus MacGillivray, Can. Ent., Vol. LV, No. 7, July, 1923, p. 159; Frison, Bull. Ill. Nat. Hist. Surv., Vol. XVI, Art. IV, Feb., 1927, p. 244. *New synonymy.*

Female.—Length 7 to 9 mm. Head black: thorax black with the prothorax, anterior lobe and tegulae rufous, legs black with the anterior knees and tibiae more or less rufous; abdomen with segments 1 to 6 rufous, apex black. The thorax may have only the prothorax rufous, or may have the lateral lobes also partly rufous. Wings almost hyaline, with a larger or smaller tawny area below stigma.

Body well clothed with white pubescence. Head somewhat variable in contour, the vertex being robust or shrunken, usually intermediate; area below vertex roughly reticulate; postocular area same length as eye, seen from above, with a distinct transverse ridge, more or less sparsely punctate and shining, and with a distinct posterior carina; vertical furrows variable, usually shallowly formed and linear, sometimes deeper; postocellar area rectangular, nearly twice as wide as long, very gently convex, only slightly raised above level of postocular area. Halves of anterior lobe moderately carinate, disk shining, densely punctured, lateral areas rough

with small punctures; lateral lobes densely punctate, shining; post-tergite triangular, densely striate, with a sharp median carina; meso-episternum more or less slightly depressed above pectus, rough with fairly large, uneven, reticulate punctures, largest in the centre of the area; pectus shining, densely punctured, diagonal row distinct; tarsal claws with a moderate tooth. Sheath usually as in Figure 33, rarely as in Figure 37, cerci three-quarters or entire dorsal length of sheath. Saw as in Figure 59; lance serrate (Figure 57); lancet with well developed lateral armature; alae, alar spines, and ventral spines prominent, spurettes large and distinct, lobes more or less anvil-shaped, without teeth.

Male.—Size 7 to 8 mm. Head and thorax black with more or less of the tegulae and front knees and tibiae rufous, abdomen with the basal six segments rufous, the remainder black. Wings as in female.

Structurally like female, except that the postocellar area is distinctly raised and the post-tergite is often smoother. Hypopygium short, wide, and almost squarely truncate. Genitalia as for group.

Lectotype.—♀, Connecticut (No. 1796). Designated in manuscript by Rohwer, October 23, 1920. In the collection of the Yale University, New Haven, Conn.

Distribution.—This form is very numerous and widespread in the following states: Connecticut, Illinois, Iowa, Massachusetts, Michigan, Minnesota, Nebraska, New Hampshire, New Jersey, New York, Ohio, Pennsylvania, South Dakota, Wisconsin, Manitoba, Ontario and Quebec. In addition the following more or less scattered records have been assembled: COLORADO: 1♂, Col.; 1♂, Boulder, May 18, 1901; 1♀, West-cliff. INDIANA: 1♀, Ind.; 1♀, E. Chicago, May 3. KANSAS: 2♀♀, Douglas County. KENTUCKY: 1♀, Russel, Sept. 7, 1928 (R. P. Johnson and C. H. Kennedy). MAINE: 1♀, Me. MISSOURI: 1♀, St. Louis. MONTANA: 1♀, Summit Station. NORTH DAKOTA: 1♀, University, June, 1896. TEXAS: 1♀, Tex. VERMONT: 1♀, Rutland, Aug. 1-5, 1916. ALBERTA: 1♀, Lethbridge, May 20, 1913 (H. L. Seamans); 1♀, Lethbridge, Aug. 5, 1923 (Gray).

In Illinois this species is found in great numbers along the railroad where the banks and right-of-way have a thick and well-established growth of grasses and horsetail (*Equisetum arvense*), breeding upon the latter. It begins to appear when *aprilis* is at the height of its numbers, and when *similis* is at its peak, *aprilis* is decidedly on the wane. Around Urbana this is usually during the latter part of April and the beginning of May. *Similis* is the only Nearctic species of this genus to be reared from the larvae (Yuasa, 1922).

Dolerus similis var. *novicius* MacGillivray

Dolerus novicius MacGillivray, Can. Ent., Vol. LV, No. 3, Mar., 1923, p. 67; Frison, Bull. Ill. Nat. Hist. Surv., Vol. XVI, Art. IV, Feb., 1927, p. 243.

Female.—Structurally like the typical form of *similis*. Differs in color in having the lateral lobes entirely rufous and more rufous on the fore-legs, often with the base of the middle tibiae rufous.

Type.—♀, Hood River, Oregon, July 28, 1914 (Childs). In the MacGillivray Collection, University of Illinois, Urbana, Ill.

Distribution.—This variety of the female is occasionally found among series of typical *similis* in its southern range. The following records have been examined: IDAHO: 1 ♀, Troy, May 31, 1908. ILLINOIS: 1 ♀, Algonquin, Jn. 16, 1909 (Nason); 2 ♀, Ogden, May 26, 1928 (Ross). MASSACHUSETTS: 1 ♀, Mass.; 1 ♀, Hampshire County. MINNESOTA: 1 ♀, Lake Vaduais, Jly. 31, 1917. MONTANA: 1 ♀, Beaver Creek. NEBRASKA: 1 ♀, Glen Sioux County, 4000 ft. alt., Jly. 13, 1910 (L. Bruner). NEW JERSEY: 1 ♀, Ramsey, Jn. 23, 1917; 1 ♀, English-town, Jly, 1923; 1 ♀, Matawan (N. Beutenmuller). NEW YORK: 1 ♀, N. Y.; 1 ♀, Van Cortlandt Park, Jn. 20, 1894. PENNSYLVANIA: 1 ♀, Lehigh Gap, Jly. 11, 1900. SOUTH DAKOTA: 2 ♀ ♀, Cutler, Jly. 18, 1924. ALBERTA: 1 ♀, Lethbridge, Jn. 1, 1922 (H. L. Seamans); 1 ♀, Lethbridge, May 20, 1923.

Dolerus similis var. *nummarius* MacGillivray

Dolerus nummarius MacGillivray, Can. Ent., Vol. LV, No. 7, July, 1923, p. 159; Frison, Bull. Ill. Nat. Hist. Surv., Vol. XVI, Art. IV, Feb., p. 243.

Female.—Structurally identical with the typical *similis*. Differs in color in having the thorax entirely black except for the front knees and sometimes an indistinct rufous spot on collar. Wings with a larger sub-stigmal area infusate.

Type.—♀, Edmonton, Alberta, June 2, 1917 (F. S. Carr). In the MacGillivray Collection, University of Illinois, Urbana, Ill.

Distribution.—This dark variety is correlated with high altitudes or northern latitudes. In the middle latitudes of the species' range it is mixed in almost equal numbers with typical *similis*, but in the northern latitudes it is present in greater numbers than any other color phase. It is common mixed with the typical form in Massachusetts, Michigan, Minnesota, New York, Manitoba, Ontario and Quebec. In addition it has been taken in the following localities: COLORADO: Ouray, 10,000 ft. alt., Walden, 8300 ft. alt., and Dolores. NEW HAMPSHIRE: Franconia. VERMONT: E. Putney, Jly. 4, 1916. WYOMING: 1 ♀, Yellowstone Park, Jly. 20, 1925 (A. A. Nichol). ALBERTA: Edmonton and Banff, in June. BRITISH COLUMBIA: Lillooett and Blue River, in June and July. MANITOBA: Winnepeg, Aweme and Birtle, from May to July. NEW BRUNSWICK: Bathurst, Jly. 6 (J. N. Knull). N. W. TERRITORY: 1 ♀, Salt River, Jn. 6–15, 1926 (J. Russell); 1 ♀, Fort Simpson, Mackenzie River, June 25, 1922 (C. H. Crickmay). SASKATCHEWAN: 1 ♀, Fort a la Corne, Jly. 17, 1925 (K. M. King).

Dolerus similis var. *tibialis* Cresson

Dolerus tibialis Cresson, Trans. Amer. Ent. Soc., Vol. VIII, 1880, p. 52; Dalla Torre, Cat. Hymen., Vol. I, 1894, p. 18.

Dolerus nervosus MacGillivray, Ins. Insc. Mens., Vol. XI, Nos. 1 to 3, 1923, p. 31; Frison, Bull. Ill. Nat. Hist. Surv., Vol. XVI, Art. IV, Feb., 1927, p. 243. *New synonymy.*

Female.—Length 9 to 10.5 mm. Head black; thorax black with the tibiae almost entirely, tegulae, and sometimes indefinite areas on mesonotum, rufous; six basal segments of abdomen rufous, apex black. Wings wholly infusate, but only moderately so, deeper at base and slightly lighter towards apex.

Structure, including genitalia, identical with *similis*, except that the halves of the anterior lobe are scarcely carinate, more nearly gently convex; and the vertical furrows are always deep and trench-like, making the postocellar area more quadrate.

Male.—Length 8.5 to 9 mm. Color and structure similar to female. Some males tend towards a melanic variety and have only the bases of the tibiae and two or three terga rufous.

Holotype.—♂, Washington Territory. In the collection of the Philadelphia Academy of Natural Sciences, Philadelphia, Pa.

Allotype.—♀, same data. Apparently from the same series from which the male was described. Deposited with the holotype. Present designation.

Distribution.—A western form, known from about 70♂♂ and 10♀♀ from the typic locality and 1♀, Colorado Lake, Oregon, May 29 (E. V. Storm), the type of *nervosus*.

Dolerus similis var. *conjectus* new variety

Female.—In size, color and structure for the most part like *tibialis* but differing in color in having the tibiae entirely black instead of rufous.

Holotype.—♀, Creston, British Columbia, May 28, 1926 (A. A. Dennys). Deposited in the Canadian National Museum, Ottawa, Canada.

Paratypes.—BRITISH COLUMBIA: 6♀♀, Creston, May 18, 1923 (C. B. Twigg); 5♀♀, Creston, Jly. 29, 1926 (A. A. Dennys); 1♀, Oliver, May 16, 1923 (C. B. Garrett); 1♀, Vernon, June 2, 1926 (E. R. Buckell); 1♀, Revelstoke, July 13, 1929 (H. H. Ross). Deposited in the collections of the Canadian National Museum, the Illinois State Natural History Survey, and the author.

Known only from the Okanagan and Kootenay River valleys in the dry belt of southern British Columbia. This variety differs from typical *similis* only in its larger size and infusate wings.

Dolerus similis subsp. *nordanus* new subspecies

Female.—Differs in color from the typical *similis* in having the head and thorax entirely black, resembling *similis nummarius*. The abdomen

has the first five segments rufous, the apex black. Wings hyaline, The head is slightly more robust behind the eyes than in the typical form, otherwise it is structurally identical with it. The sheath is of the longer (*plesius*) type (Figure 38), and is midway between the short-sheathed *nummarius* and the typical form of *aprilis* in this regard.

Male.—Similar to the typical form, and inseparable from it.

Holotype.—♀, Lethbridge, Alberta, May 20, 1923 (E. H. Strickland). Deposited in the collection of the Illinois State Natural History Survey, Urbana, Ill.

Allotype.—♂, Lethbridge, Alberta, May 6, 1923 (E. H. Strickland). Deposited with holotype.

Paratypes.—ALBERTA: 1♂, 6♀♀, Lethbridge, May 6 to 24, 1923 (E. H. Strickland); 6♀♀, Lethbridge, May 2 to 20, 1922 and 1923 (H. L. Seamans); 1♀, Lethbridge, May 10, 1923 (Walter Carter); 1♀, Banff, May 26, 1922 (C. B. Garrett). BRITISH COLUMBIA: 1♀, Oliver, May 8, 1923 (B. C. Garrett). WASHINGTON: 1♀, Pullman, May 15, 1901 (C. V. Piper); 1♀, Pullman (C. V. Piper). NEVADA: 1♀, Nev. In the collections of the U. S. National Museum, the Canadian National Museum, the University of Alberta, the Illinois State Natural History Survey, and the author.

This form, taken in the west and northwest, resembles *similis nummarius* and *aprilis* in color, and is separated from them only on the proportions of the sheath. The females of *similis* with the black thorax from these regions possess the longer sheath with great constancy.

Dolerus similis subsp. *fumatus* new subspecies

Female.—Differs from *similis nordanus* only in having the wings uniformly brown infusate.

Male.—Similar to female. Indistinguishable from the males of *similis coniectus* and dark-winged forms of *similis simulans*.

Holotype.—♀, Starbuck, Washington, April 10, 1923 (M. C. Lane). In the U. S. National Museum, Washington, D. C.

Allotype.—♂, same data as holotype. Deposited with it.

Paratypes.—WASHINGTON: 5♂♂, 5♀♀, same data as holotype; 1♀, Walla Walla, May. CALIFORNIA: 3♀♀, Portola, June 5, 1915 (M. C. Van Duzee). UTAH: 1♀, Utah L. In the MacGillivray Collection, and the collections of the U. S. National Museum, the Illinois State Natural History Survey, and the author.

This form has been taken only on the Pacific Coast. Like *similis nordanus*, the sheath is of the long form upon which character it may be separated from *similis coniectus*.

Dolerus similis subsp. *simulans* Rohwer

Dolerus simulans Rohwer, Can. Ent., Vol. XLI, No. 1, Jan., 1909, p. 10.

Female.—Length 7.5 to 9 mm. Head black, thorax black with the prothorax, anterior and lateral lobes and tegulae rufous, legs black, abdomen rufous except more or less of apical two or three segments which may be black. Anterior lobe sometimes with a median triangular black area, variable in size and extent. Wings uniformly tawny infusate, sometimes very lightly, sometimes darkly so.

Structure almost identical with typical *similis*, with the following differences: halves of anterior lobe not so carinate, but slightly so; lateral lobes a trifle less densely punctate. Genitalia identical with the typical form.

Male.—7. to 7.5 mm. in length. Color entirely black except the six basal segments which are rufous. Tegulae black, legs black except a minute light ring at the apices of the front femora. Wings hyaline or lightly, evenly infusate.

Structure as in female. Differs slightly from the typical *similis* in usually having the postocular area more densely punctate.

Lectotype.—♀, Florissant, Colorado, June 2, 1907. Labelled by the describer as type at the time of preparation of the original description. Deposited in the U. S. National Museum, Washington, D. C.

Allotype.—♂, Ute Creek, Colorado, 9000 ft. alt., June 24, (L. Bruner.) In the collection of the University of Nebraska, Lincoln, Neb. Present designation.

Distribution.—COLORADO: Ute Creek, 9000 ft. alt., Florissant, West-cliff, Black Lake, Bondad (6100 ft. alt.), Monte Vista (7650 ft. alt.), Durango, Colden and Electra Lake (8400 ft. alt.), from May to July. IDAHO: 1♂, 1♀, Bovil, Jn. 17, 1911; 1♂, Moscow Mt., June 3, 1911; 1♂, Giveout (8700 ft. alt.), July 7, 1920. MONTANA: ♂♂ and ♀♀, Helen, Gallatin County, Missoula County, and Florence, June and July. NEVADA: 1♂, 1♀, Nev. NEW MEXICO: 1♂, 2♀♀, Jemez Springs, 8500 ft. alt., June 19, 1916 (J. Woodgate); 3♂, Fort Wingate, May 14, 1908 (J. Woodgate); 1♂, San Ignacio, June (Cockerell). UTAH: 1♀, Riverdale (Weber River), June, 1926 (C. J. D. Brown); 1♀, Farr West, (V. M. Tanner). WASHINGTON: 2♂♂, 7♀♀, Pullman, May 12 to June 14. WYOMING: 1♀, Fort Bridger, June, 1926.

This form is essentially western in distribution. The combination of the rufous lateral lobes and black, or almost black, knees, the occurrence of a black area on the anterior lobe and the slightly smaller size, separate this form from other forms of *similis*. In the absence of constant structural differences, however, and from the appearance of blackish forms which merge into *similis nummarius*, it does not seem well enough differentiated to be called a distinct species.

Dolerus similis subsp. *nescius* MacGillivray

Dolerus nescius MacGillivray, Univ. Ill. Bull., Vol. XX, No. 50, Aug. 13, 1923, p. 12; Frison, Bull. Ill. Nat. Hist. Surv., Vol. XVI, Art. IV, Feb., 1927, p. 243.

Female.—Length 9.5 to 10.5 mm. Head black; thorax black, with the prothorax, anterior and lateral lobes, tegulae and sometimes front tibiae, rufous; abdomen rufous with the sheath black. Wings lightly infusate, deeper along the veins and at base of wing.

Structurally almost identical with *similis*, with the following differences: transverse ridge of postocular area very sparsely punctate, polished; vertical furrows deep; disk of anterior lobe, lateral lobes and pectus only sparsely punctate; post-tergite sometimes nearly smooth, but usually closely striate; sheath as in Figure 37, saw as in *similis* (Figure 59).

Male.—Length 8.5 to 9 mm. Body entirely black except terga 2 to 6 and sterna 1 to 7, which are rufous. Wings moderately tawny infusate, darker at base.

Structure similar to female, genitalia as for group.

Type.—♀, Kendrick, Idaho, April 14, 1900 (J. M. Aldrich). In the MacGillivray Collection, University of Illinois, Urbana, Ill.

Allotype.—♂, Oliver, British Columbia, May 11, 1923 (C. B. Garrett). Deposited in the Canadian National Museum, Ottawa, Canada. Present designation.

Distribution.—NEVADA: 1♂, 8♀♀, Elko. WASHINGTON: 1♀, Spangle, May 24, 1898. BRITISH COLUMBIA: 3♂♂, 4♀♀, Oliver, May 2 to Aug. 10, 1923 (C. B. Garrett); 1♂, Vernon, May 3, 1903; 1♀, Fairview, Apr. 28, 1919 (E. R. Buckell) 1♀, Fairview, May 18, 1919 (E. R. Buckell); 1♀, Penticton, May 20, 1919 (E. R. Buckell).

This subspecies occurs on the western Rocky Mountain slope. It is separated from other forms of *similis* by its large size, entirely rufous abdomen and thoracic lobes, and fuscous wings. It may be confused with *coloradensis*, but can be readily separated from it by the densely punctate sides of the anterior lobe, and in the female by the black meso-episternum.

Dolerus nicaeus MacGillivray

Dolerus nicaeus MacGillivray, Can. Ent., Vol. LV, No. 3, Mar., 1923, p. 68; Frison, Bull. Ill. Nat. Hist. Surv., Vol. XVI, Art. IV, Feb., 1927, p. 243.

Dolerus nimbosus MacGillivray, Ins. Insc. Mens., Vol. XI, Nos. 1 to 3, 1923, p. 33; Frison, Bull. Ill. Nat. Hist. Surv., Vol. XVI, Art. IV, Feb., 1927, p. 243. *New synonymy*.

Dolerus necessarius MacGillivray, Ins. Insc. Mens., Vol. XI, Nos. 1 to 3, 1923, p. 35; Frison, Bull. Ill. Nat. Hist. Surv., Vol. XVI, Art. IV, Feb., 1927, p. 242. *New synonymy*.

Female.—Length 7.5 to 9 mm. Color entirely black. Wings hyaline.

Structure identical with *similis*, with the following differences: postocular area usually slightly shrunken, not robust, the transverse ridge either shining or punctate; post-tergite usually distinctly striate, but sometimes indistinctly so. Genitalia as in Figures 34 or 38, and 59.

Male.—Length 7 to 8 mm. Color and structure similar to female, but with postocular area usually densely punctate with only a small shining area. Genitalia as for group.

Type.—♀, Chilliwack, Cultus Lake, British Columbia, May 31,—(F. C. Ewing). In the MacGillivray Collection, University of Illinois, Urbana, Ill.

Allotype.—♂, Corvallis, Oregon, April 8, 1928 (H. A. Scullen). Deposited in the collection of the Illinois State Natural History Survey, Urbana, Ill. Present designation.

Distribution.—IDAHO: 1 ♀, Moscow. OREGON: ♂♂ and ♀♀, Corvallis, Oregon City, Marion, King's Valley, Eugene, from April to August. WASHINGTON: 4 ♂♂, 3 ♀♀, Pullman, April and May. BRITISH COLUMBIA: ♂♂ and ♀♀, Vancouver, Agassiz, Chilliwack, Victoria, Huntingdon, Penticton, Post Hammond, Cranbrook, Okanagan, from May to July. ALASKA: 1 ♂, Berg Bay, June 10, 1899 (T. Kincaid).

This is the commonest species of *Dolerus* in the humid wet belt of the Pacific Coast. It is separated from members of the *sericeus* group by its rotund hind tibiae, from *elderi melanus* by its larger size, rougher postocular area and different type of punctuation of the pleurae, and from *nasutus*, which it closely resembles, by the rougher and punctate postocular area, having no bluish tinge to the area between the eyes and ocelli, the meso-episternum having rough and more or less unequal punctures, the pectus being densely but finely punctate adjacent to the pleurae, and in the female by the wider sheath with the distinct lateral carina. *Neopaprilis konowi* differs in the very deeply depressed pleurae and longer hypopygium, and *neocollaris narratus* in the long postocular area.

Dolerus aprilis (Norton)

Dosytheus aprilis Norton, Proc. Boston Soc. Nat. Hist., Vol. VIII, 1861, p. 152; Cresson, Proc. Ent. Soc. Philadelphia, Vol. IV, 1865, p. 243.

Dolerus aprilis Norton, Trans. Amer. Ent. Soc., Vol. I, 1867, p. 236; Provancher, Nat. Canad., Vol. X, 1878, p. 71; Provancher, Faun. Ent. Can., Hymen., 1883, p. 197; Dalla Torre, Cat. Hymen., Vol. I, 1894, p. 3; MacGillivray, Bull. 22, Conn. Geol. Nat. Hist. Surv., 1916, p. 74.

Dolerus dysporus MacGillivray, Can. Ent., Vol. XL, No. 4, April, 1908, p. 128; Frison, Bull. Ill. Nat. Hist. Surv., Vol. XVI, Art. IV, Feb., 1927, p. 241. *New synonymy*.

Female.—Length 8 to 9 mm. Head and thorax, including legs, black, abdomen rufous with apical three segments black. Wings hyaline, sometimes with an infusate area in centre or at apex of wing.

Structurally almost identical with *similis*, differing slightly as follows: transverse ridge of postocular area usually densely punctate; meso-episternum with more linear and slightly larger punctures. Sheath long and rhomboidal (Figure 39), very black, posterior margin oblique, forming an angle with ventral margin; cerci never attaining more than one-half length of sheath; saw similar to *similis*, usually having the alae a little larger in the central region of the saw.

Male.—Averages a millimetre longer than *similis*; practically identical with *similis*, usually differing as follows: postocular area flatter, dull and punctate, without a shining transverse ridge; anterior lobe more densely punctate on disk, more coarsely on sides. These differences frequently break down, and it is often impossible to separate the males of these two species.

Neotype.—♀, Seymour, Illinois, April 15, 1929 (Frison and Ross). Deposited in the collection of the Illinois State Natural History Survey, Urbana, Ill.

Distribution.—Specimens of this species have been examined from the following localities: COLORADO: Florissant. CONNECTICUT: Cornwall. ILLINOIS: Algonquin, Urbana, Seymour, Savoy, Chebanse, Loda, Ashkum, White Heath, St. Joseph, Ogden, Adair, Macomb, Bryant and Pleasant Plains. IOWA: Mt. Pleasant. MASSACHUSETTS: Beverly, Chicopee, Amherst, Lawrence, Arlington. MICHIGAN: Douglas Lake, Ann Arbor. MINNESOTA: St. Paul. NEW HAMPSHIRE: Franconia. NEW JERSEY: Clementon, Snake Hill. NEW YORK: Ithaca Palisades, Richfield Springs, Albany, Potsdam, Bethlehem, New York City, Utica, Flushing and White Plains. OHIO: Ohio. PENNSYLVANIA: Conawego. VIRGINIA: Fort Monroe. ONTARIO: Ottawa. QUEBEC: Montreal, St. Hilaire.

This species occurs in its greatest abundance in April and May, with occasional records in June and August. It is usually a fairly rare species in collections, but in the *Dolerus* habitats around Urbana was taken in great numbers during the last two weeks of April. It came into the picture earlier than *similis*, which took its place later in the season after *aprilis* had declined in numbers. It occurs throughout the eastern and central part of the continent, and probably is as numerous as *similis* in most habitats, but has not yet been taken in large numbers because of a lack of early collecting.

In the female the color of the body and shape of the sheath are easily recognizable features of this species. The male runs down with *similis*, and, as stated in the description, is not easy to separate from it.

Dolerus aprilis var. *nocivus* MacGillivray

Dolerus nocivus MacGillivray, Univ. Ill. Bull., Vol. XX, No. 50, Aug. 13, 1923, p. 12; Frison, Bull. Ill. Nat. Hist. Surv., Vol. XVI, Art. IV, Feb., 1927, p. 243.

Female.—Structurally identical with the typical form. Differs in color as follows: thorax with the prothorax, anterior lobe, tegulae, upper portion of meso-episternum, front knees and sometimes a posterior spot on the lateral lobes, rufous. Wings as in the typical form.

Type.—♀, Ames, Iowa, May 12, 1918 (H. A. Scullen). In the MacGillivray Collection, University of Illinois, Urbana, Ill.

Distribution.—Only the following records have been assembled from material other than that taken in Illinois: IOWA; 1 ♀, Mt. Pleasant, May 5, 1926. NEW YORK: 2 ♀, Ithaca, April and May; 1 ♀, Richfield Springs. SASKATCHEWAN: 1 ♀, Oxbow, June 18, 1907 (F. K. Knab). Several hundred specimens have been taken in Illinois from the following localities: Danville, Muncie, White Heath, Algonquin, Seymour, St. Joseph, Ogden, Savoy, Loda, Chebanse, Ashkum, Urbana, Canton, Adair, Macomb, Pleasant Plains, Sparland and Woodford. In Illinois this variety has slightly outnumbered the typical form, the two being taken together at almost all the localities without respect to advance of season. This form has usually been identified as *similis*, but may be easily separated from it by the long, rhomboidal sheath and the short cerci.

Dolerus coloradensis Cresson

Dolerus coloradensis Cresson, Trans. Amer. Ent. Soc., Vol. VIII, 1880, p. 11; Dalla Torre Cat. Hymen., Vol. I, 1894, p. 4; Rohwer, Can. Ent., Vol. XLI, No. 1, Jan., 1909, p. 11; Cresson, Mem. Amer. Ent. Soc., No. 1, 1916, p. 4.

Dolerus tejonensis Weldon, Can. Ent., Vol. XXXIX, No. 4, Sept., 1907, p. 303.

Female.—Length 9.5 to 11.5 mm. Head black, sometimes with the clypeus entirely or partly rufous; thorax mostly rufous with the scutum, post-tergite, part of posterior margin of metathorax, all or the median half of pectus, sometimes margins of meso-episternum, meso-epimeron entirely, most of metapleurae, and legs entirely, black; abdomen rufous except sheath which is black. Wings moderately to deeply infusate.

Proportions of head and antennae as for *similis*. Structurally very similar, but with a greatly reduced punctuation; postocular area shining, almost imperceptibly punctate, posterior margin with a rounded, distinct carina; postocellar area shining, fairly densely punctate; both anterior and lateral lobes polished, evenly minutely punctate; post-tergite triangular, striate and sharply carinate; pleurae and pectus shining, pleurae with large, smooth punctures, pectus polished, very minutely punctate. Genitalia as for *similis*.

Male.—Length 9 to 10 mm. Head and thorax entirely black, abdomen rufous except apical segment which is black.

Structure as in female, genitalia as for group.

Type.—♀, Colorado. In the collection of the Academy of Natural Sciences, Philadelphia, Pa.

Distribution.—COLORADO: 6 ♂♂, 14 ♀♀, Col.; 3 ♂♂, 2 ♀♀, Ute Creek, Jly. 11 to Aug. 1 (R. W. Dawson); 1 ♀, Fort Collins; 1 ♂, 2 ♀♀, Westcliff; 1 ♀, Monte Vista, 7650 ft. alt., Jn. 16, 1919; 2 ♂♂, 1 ♀, Fort Collins, Jn. 13, 1901; 1 ♂, Livermore; 2 ♀♀, Estes Park. MONTANA: 5 ♂♂, 4 ♀♀, Mon.; 1 ♂, East Flathead, 5700 ft. alt., Jly. 25, 1902; 1 ♀, Bozeman, 4400 ft. alt., Jn. 13, 1903; 1 ♀, Gallatin County, Jn. 17, 1904;

1 ♀, Jefferson County, May 22, 1926. NEW MEXICO: 1 ♀, Las Vegas, Mar. 3 (Barber and Schwarz); 1 ♀, Peco, Jly. 13 (T. D. A. Cockerell). WYOMING: 1 ♂, Cheyenne (C. V. Riley).

This species may be separated from *similis nescius* by having the sides of the anterior lobe impunctate, polished, and from *tejonensis*, with which it has often been confused, by the punctate postocular area, the punctate scutum, punctures of the meso-episternum being rough, close and reticulate, with sharp walls, the shape of the saw in the female, and the black thorax and the apex of the abdomen in the male.

Dolerus tejonensis (Norton)

Dosylheus tejonensis Norton, Proc. Boston Soc. Nat. Hist., Vol. VIII, 1861, p. 154.

Dolerus tejonensis Norton, Trans. Amer. Ent. Soc., Vol. I, 1867, p. 239; Dalla Torre, Cat.

Hymen., Vol. I, 1894, p. 17; Rohwer, Can. Ent., Vol. XLI, No. 1, Jan., 1909, p. 11.

Dolerus coccinifera Norton, Trans. Amer. Ent. Soc., Vol. IV, 1872, p. 82; Cresson, *ibid*, Vol.

VIII, 1880, p. 34; Cresson, Mem. Amer. Ent. Soc., No. 5, 1928, p. 5. *New synonymy*.

Dolerus coccinifer Dalla Torre, Cat. Hymen., Vol. I, 1894, p. 4.

Female.—Length 10.5 to 12 mm. Head black; thorax rufous, except pectus, legs, and usually meso-episternum entirely, but sometimes only the lower portion, and sometimes a small median area on anterior lobe, black; abdomen rufous except sheath which is black. Wings deeply infusate, violaceous.

Head below vertex roughly reticulate, vertex polished, minutely and sparsely punctured; postocular area length of eye, seen from above, with a small transverse ridge, and a posterior carina; vertical furrows very wide, deep; postocellar area quadrate, very convex and prominent; antennal lengths as in *similis*, but each segment slightly narrower at the base, giving a more or less doubly serrate appearance. Anterior and lateral lobes and pectus very highly polished, impunctate except for one or two very minute pits; tarsal claws with a medium-sized tooth. Sheath as in Figure 37; saw after the same fashion as *similis*, but differs as follows: lance scalloped, not serrate; alae large, alar spurs very large, somewhat blunt, ventral spines reduced; spurettes distinct; lobes with several rounded teeth (Figure 60).

Male.—Length 11 to 12 mm. Head black; dorsum of thorax entirely rufous or with anterior lobe and scutum black; pectus, pleurae and legs black; abdomen rufous. Wings violaceous.

Structure similar to female. Clypeus usually normal but sometimes almost truncate, or slightly sinuate. Hypopygium with sides of apex slightly convex, apical margin slightly concave. Genitalia differing from the group type in having the apices of the praeputium widely spreading, and the gonocardo a thin band of equal width for its entire length. The base of the praeputium is even less pointed than in Figure 68.

Lectotype.—♀, Fort Tejon, California. In the collection of the Academy of Natural Sciences, Philadelphia, Pa. This old specimen was found in the undetermined duplicates in the collection of the Academy at Philadelphia, and bore a small hand-printed label "Ft. Tejon, Cal.", and beneath it a larger label with a red ink border with the handwriting "*Dolerus tejonensis* Norton." Since the specimens from which he drew up the description of this species, and which he stated belonged to the Smithsonian Institute, can not be found in that institution, it has been assumed that this specimen is one of the two originally examined by Norton, and it has been remounted on a modern pin and designated as the lectotype.

Distribution.—Restricted to the southwestern corner of the United States. Specimens have been examined from the following localities: CALIFORNIA: ♂♂ and ♀♀, Alameda County, Los Angeles County, San Jacinto Mts., Soda Springs, Lundy (8000 ft. alt.), Shasta, Redlands, Ventura County, Fort Tejon, Woyden, San Diego, Sacramento, Topico, from March to October. NEVADA: 10♂♂, 2♀♀, Nev.; 1♂, Reno. NEW MEXICO: 1♀, Alamogordo, May 12, 1902. UTAH: 1♀, Ut.

The only species with which this is likely to be confused is *coloradensis*, from which it may be separated in the female by the very convex and shining postocellar area and anterior lobes, the polished and practically impunctate scutum, the punctures of the meso-episternum being separated by wide and polished walls, the meso-episternum merging smoothly into the pectus, and the saw; and in the male by the rufous on the dorsum of the thorax and by the entirely rufous abdomen.

The male genitalia of this species are almost intermediate in proportion between the *similis* and *neoaprilis* groups, but the saw shows very decided affinities with the *similis* group, so the species is placed with the latter.

NEOAPRILIS GROUP

This group was erected for the single species *neoaprilis*, the genital characters of which separate the group from other members of the genus.

Dolerus neoaprilis MacGillivray

Dolerus neoaprilis MacGillivray, Can. Ent., Vol. XL, No. 4, April, 1908, p. 126; MacGillivray Bull. 22, Conn. Geol. Nat. Hist. Surv., 1916, p. 70; Frison, Bull. Ill. Nat. Hist. Surv., Vol. XVI, Art. IV, Feb., 1927, p. 242.

Dolerus nivatus MacGillivray, Jour. N. Y. Ent. Soc., Vol. XXXI, No. 4, Dec., 1923, p. 164; Frison, Bull. Ill. Nat. Hist. Surv., Vol. XVI, Art. IV, Feb., 1927, p. 243. *New synonymy*.

Female.—Length 9 to 12 mm. Body black, with the front knees and from two to six abdominal segments rufous. Wings hyaline, faintly stained below stigma and towards apex.

Head below vertex very rough; clypeus very deeply notched, cleft one-half its length; postocular area length of eye, seen from above, robust,

but narrower than width of head through eyes; with a low transverse ridge and a distinct posterior carina; the transverse ridge shining and sparsely punctured, and the region near the lateral ocelli shagreened; vertical furrows linear and indistinct or shallow and trough-shaped; post-ocellar area quadrate, only slightly convex, and but a little raised above level of postocular area, shining, with fairly large punctures; antennae filiform, slightly bilaterally compressed near base, third segment a little longer than fourth, remainder almost equal. Mesonotum densely punctured; disk of anterior lobe shining, with fairly large punctures, sides with large, rugose punctures; halves of anterior lobe convex, not carinate; lateral lobes dull, disk more sparsely punctate than remainder; post-tergite stocky in outline, shining, unstriate or granularly so, striations rounded, not sharp, median carina only on basal (=anterior) half, posterior margin rounded; meso-episternum deeply depressed above pectus, very coarsely and roughly rugose, rugosities maintaining their size to margin of pectus; pectus very sharply set off from pleurae, slightly concave laterally, dull, shagreened and closely punctured, sometimes slightly glossy; diagonal row wanting; tarsal claws with a fairly large tooth. Sheath stocky in appearance (Figure 36), ventral margin uniformly convex, dorsal margin convex or appearing nearly straight, lateral face with a strong carina at base, usually fading before reaching apical half of sheath but sometimes suggested for the entire length by the contour; sheath clothed with short, black, stiff setae, tufted at apex, a few lateral ones slightly longer and curved; cerci attaining one-half to three-quarters length of sheath. Saw as in Figure 3; lance scalloped, not serrate; lancet with alae and alar spurs large and distinct, lacking alar spines but with ventral spines, spurettes large and separate, lobes step-like, minutely dentate.

Male.—Length 7.5 to 10 mm. Color and structure as in female, with the following differences in structure: third and fourth antennal segments equal, flagellum regularly setaceous; halves of anterior lobe more sharply convex, lateral portions more finely punctured; hypopygium very long and large, very convex ventrally, sides of apex concave, apex almost truncate, fairly narrow.

Type.—♀, Nebraska (F. Rauterberger). In the MacGillivray Collection, University of Illinois, Urbana, Ill.

Allotype.—♂, Seymour, Illinois, April 15, 1929 (Frison and Ross). Deposited in the collection of the Illinois State Natural History Survey, Urbana, Ill. Present designation.

Distribution.—COLORADO: 1 ♀, Garland; 1 ♀, Veta Pass. ILLINOIS: 1 ♀, Seymour, Apr. 14, 1929 (Park and Ross); 2 ♂♂, Seymour, Apr. 15, 1929 (Frison and Ross); 1 ♂, Muncie, Apr. 16, 1929 (Frison and Ross); 1 ♂, 2 ♀♀, Adair, May 4, 1929 (T. H. Frison); 1 ♂, Pleasant Plains,

May 2, 1929 (T. H. Frison); many ♂♂, ♀♀, Sherman, April 2, and Dixon, Garden City and Grand Detour, May 15-16, 1930 (Frison and Ross). IOWA: 1 ♀, Mt. Pleasant, May 5, 1926. MASSACHUSETTS: 1 ♀, Springfield, May 4, 1903 (F. K. Knab). MICHIGAN: 2 ♀♀, Cheboygan County, June, 1928 (C. H. Kennedy). MINNESOTA: 1 ♀, St. Paul, June 7, 1911. NEW HAMPSHIRE: 1 ♀, N. H.; 1 ♂, 1 ♀, Franconia; 1 ♀, Mt. Washington. NEW YORK: 1 ♀, Utica; 2 ♀♀, Newport, June 26, 1902; 1 ♀, Albany, May 23, 1903. SOUTH DAKOTA: 2 ♀♀, Brookings; 1 ♀, Englewood, June 18, 1925. ALBERTA: 3 ♀♀, Banff, June 1, 1922 (C. B. Garrett). BRITISH COLUMBIA: 1 ♀, Blue River, Jly-Aug., 1926 (W. F. McCullough). MANITOBA: 3 ♀♀, Aweme, June and July, (Criddle and Bird); 1 ♀, Treesbank, June 26, 1926 (R. D. Bird); 1 ♂, Birtle, May 30, 1928 (R. D. Bird). N. W. TERRITORY: 1 ♀, Ft. Providence, Mackenzie River, Jly. 8, 1903 (Mack); 1 ♀, Ft. Simpson, Mackenzie River, June 25, 1922 (C. H. Crickmay). NOVA SCOTIA: 1 ♀, Bridgetown, June 11, 1913 (G. E. Saunders); 1 ♀, Truro, Jly. 4, 1913 (R. Matheson). ONTARIO: 1 ♀, Nipigon, June 19, 1913 (F. M. Walker); 2 ♂♂, 1 ♀, Sudbury; 1 ♀, Hillier, Nov. 10, 1911 (Evans). QUEBEC: 2 ♀♀, Megantic, June 2, 1923 (C. H. Curran); 1 ♀, Ft. Coulonge, June 11, 1918 (J. L. Beaulne); 1 ♀, Lanoraie, June 18, 1915 (Beaulne); 1 ♀, Shawbridge, May 28, 1922 (J. W. Buckle). ALASKA: 2 ♀♀, Kukak Bay, Jly. 4, 1899 (T. Kincaid); 2 ♀♀, Orea, June 27, 1899 (T. Kincaid); 2 ♂♂, 1 ♀, Yakutat, May 26 to July 4, 1899 (T. Kincaid); 1 ♂, Katmai, Jly. 19, 1919 (A. E. Miller).

Apparently a wide-spread northern species which has also been taken in large numbers in certain localities along the railroads in Illinois.

The female of this species is at once separated from all others in the genus by the peculiar sheath with the black, bristly setae, and by the saw. It is also characterized by the deeply emarginate clypeus and the depressed pleurae with the ridge-like boundaries. The male can be separated from the members of the *similis* group which it resembles in color by the deeply cleft clypeus, the rugose and depressed pleurae with the sharp walls around the depression, and the longer and more convex hypopygium. It is separated from *frisoni* by lacking a procidentia and from *apriloides* by having the walls of the depression of the pleurae sharp and not obscured by large rugosities.

Dolerus neoaprilis subsp. *konowi* MacGillivray

Dolerus konowi MacGillivray, Can. Ent., Vol. XLVI, No. 3, Mar., 1914, p. 106; Frison, Bull. Ill. Nat. Hist. Surv., Vol. XVI, Art. IV, Feb., 1927, p. 241.

Dolerus numerosus MacGillivray, Can. Ent., Vol. LV, No. 3, Mar., 1923, p. 67; Frison, Bull. Ill. Nat. Hist. Surv., Vol. XVI, Art. IV, Feb., 1927, p. 243. *New synonymy*.

Dolerus nidulus MacGillivray, Ins. Insc. Mens., Vol. XI, Nos. 1 to 3, 1923, p. 31; Frison, Bull. Ill. Nat. Hist. Surv., Vol. XVI, Art. IV, Feb., 1927, p. 243. *New synonymy*.

Both sexes structurally identical with typical *neoaprilis*, differing only in being entirely black.

Type.—♀, Olympia, Washington, June 20, 1893 (T. Kincaid). In the MacGillivray Collection, University of Illinois, Urbana, Ill.

Lectoallotype.—♂, Olympia, Washington, April 20, 1894 (T. Kincaid). In the MacGillivray Collection, University of Illinois, Urbana, Ill. (Frison, 1927).

Distribution.—CALIFORNIA: 1 ♀, Strawberry, Jly. 6, 1919. IDAHO: 1 ♀, Kendrick, Apr. 4, 1908; 3 ♀ ♀, Moore's Lake, Jly. 10, 1907. OREGON: 1 ♀, Ore.; 1 ♀, Forest Grove; 3 ♀ ♀, Waldport, Apr. 23, 1926 (J. E. Davis); 2 ♀ ♀, Corvallis. BRITISH COLUMBIA: ♂♂ and ♀ ♀, Agassiz, Port Hammond, Chilliwack, Hedley, Vancouver, Royal Oak, Metlakatla, Victoria, Prince Rupert, taken in April and May.

A melanic race of *neoaprilis* occurring solely on the Pacific slope. It is usually taken with *nicaeus* and *nasutus*, with which it agrees in color. From these and all other black species, however, it can be distinguished in the female by the sheath and saw, in the male by the long, convex hypopygium, and in both sexes by the depressed and rugose pleurae and the deeply cleft clypeus.

FRISONI GROUP

Erected to accommodate the single species *frisoni*.

Dolerus frisoni new species

Male.—Length 11 mm. Head and thorax black, except tegulae and front tibiae and basitarsus and middle tibiae, which are rufous; abdomen rufous with apex of segment six and the remaining apical segments black. Wings hyaline.

Structure somewhat similar to *apriloides* and *neoaprilis*. Head, except vertex, closely reticulate; robust, but narrowed behind eye; postocular area slightly shorter than eye, seen from above, with a rounded, transverse ridge, posterior margin feebly carinate; the median portion flat, sparsely punctate and dull, the posterior portion closely punctate; vertical furrows moderately deep, narrow and linear; postocellar area quadrate, scarcely convex, sparsely punctate and dull; clypeus notched about half its length; flagellum of antenna thick, slightly compressed at base, first three segments subequal, remainder very gradually decreasing towards apex. Disk of anterior lobe densely punctate and dull, sides densely punctate with two or three large rugosities on the lateral corner; lateral lobes moderately densely punctured, dull; post-tergite subcrescentic, stout, shining, with a few polished striations, rounded on the meson, but not carinate; meso-episternum with extremely large, irregular rugosities, very rough in appearance, fairly deeply depressed above pectus, posterior

wall of depression ridge-like and distinct, ventral and anterior walls indefinite, obscured by the large rugosities; pectus very sharply defined, densely punctate and shagreened; diagonal row fairly distinct, linear; hind tibiae not longitudinally grooved; tarsal claws with a moderate tooth two-thirds distance from base. Eighth tergite with a median procidentia extending the whole length of the segment, gradually ascending from the base, sharply carinate, with a small elevation at apex; hypopygium long, wide and convex, lateral margins concave, apical margin concave, angles rounded. Genitalia as in Figure 69; praepitium with a narrow apical cleft, apices large, wide and long; gonocardo fairly wide, narrowed on the meson; pedes narrow, sides parallel, apices rounded.

Holotype.—♀, Cook County, Illinois (E. B. Chope). In the collection of the Field Museum for Natural History, Chicago, Ill.

Known only from the holotype. It may be readily separated from all other species of the genus by the combination of a rufous abdomen with a procidentia on the eighth tergite, and by the depressed pleurae, with the largest rugosities that are found in the nearctic members of the genus. The relationship of this species is not clear, for the procidentia suggests the *sericeus* group, and the punctuation, clypeus and genitalia show distinct affinities to the *neoaprilis* group. Until the female is discovered and the saw characters are known, it seems best to place this group close to the *neoaprilis* group, following chiefly the evidence of punctuation and the genitalia.

This unique species is named in honor of Dr. T. H. Frison who has contributed such a great deal to the completion of this paper.

SUBGENUS *Loderus* Konow

Dosytheus Cresson, Proc. Ent. Soc. Phil., Vol. 1, Aug., 1861, p. 37.

Dolerus Sectio I (*Dosytheus*) Thomson, Hymen. Scand., Tom. I, 1871, p. 279.

Loderus Konow, Deut. Ent. Zeits., Vol. 34, 1890, p. 240.

Loderus Ashmead, Can. Ent., Vol. XXX, No. 12, Dec., 1898, p. 306.

Loderus Konow, Gen. Insectorum, Hymen., Fam. Tenth., 1905, p. 110 and 115.

Loderus Enslin, Deut. Ent. Zeits., Beiheft, 1913, p. 157.

Loderus MacGillivray, Bull. No. 22, Conn. Geol. Nat. Hist. Surv., 1916, p. 76.

Eyes long, distinctly emarginate on their mesal margin; malar space short, usually less than half the length of first antennal segment, but in *L. acidus* MacG. sometimes nearly as long as first segment. Face clad with dense, fine pile, clypeus partly piceous or whitish in the nearctic species which are partly rufous; vertex shining, at most sparsely punctate. Tarsal claws either without a tooth or with a small one, in the female never as large as in *Dolerus s. st.*

Genotype.—*Tenthredo pratorum* Fallen (original designation by Konow, 1890.).

KEY FOR THE SEPARATION OF THE NEARCTIC SPECIES

1. Body entirely black.....*napaeus* MacG.
- Abdomen and legs partly rufous.....2
2. Pleurae coarsely pitted, punctures round and distinct; vertical furrows trough-like and distinct.....3
- Pleurae finely cribrately punctured; vertical furrows line-like, almost obsolete.....4
3. Middle femora rufous.....*apricus* (Nort.)
- Middle femora black.....*apricus* var. *alticinctus* MacG.
4. Females (abdomen with an apical sheath-like structure, Figure 1).....5
- Males (abdomen with a flat and entire apical sternite, Figure 7).....7
5. Sheath small, evenly rounded on the ventral margin, as wide as long....*albifrons* (Nort.)
- Sheath large and projecting, straight on ventral margin, longer than wide, with a distinct small hook at the ventro-apical angle.....*acidus* MacG.
6. Third and fourth antennal segments almost equal; white spot below bases of antennae, clypeus white.....*albifrons* (Nort.)
- Third segment about one-quarter longer than fourth; white spot below antennae lacking, clypeus black in middle at base, white appearing as lateral marks.....*acidus* MacG.

Dolerus apricus (Norton)

Dolerus apricus Say, Harris Catalogue, *nomen nudum*; Norton, Trans. Amer. Ent. Soc., Vol. I, 1867, p. 236; Provancher, Nat. Canad., Vol. X, 1887, p. 71; Provancher, Faun. Ent. Can., Hymen., 1883, p. 197; Dalla Torre, Cat. Hymen., Vol. I, 1894, p. 3; MacGillivray, Bull. 22, Conn. Geol. Nat. Hist. Surv., 1916, p. 72.

Dosytheus apricus Norton, Proc. Boston Soc. Nat. Hist., Vol. XIII, 1861, p. 152.

Dolerus luctatus MacGillivray, Can. Ent., Vol. XL, No. 4, April, 1908, p. 127; MacGillivray, Bull. 22, Conn. Geol. Nat. Hist. Surv., 1916, p. 71; Frison, Bull. Ill. Nat. Hist. Surv., Vol. XVI, Art. IV, Feb., 1927, p. 241. *New synonymy*.

Dolerus femur-rubrum Rohwer, Can. Ent., Vol. XLI, No. 1, Jan., 1909, p. 9. *New synonymy*.

Loderus albifrons MacGillivray, Bull. 22, Conn. Geol. Nat. Hist. Surv., 1916, p. 76.

Loderus acerbus MacGillivray, Univ. Ill. Bull., Vol. XX, No. 50, August 13, 1923, p. 19; Frison, Bull. Ill. Nat. Hist. Surv., Vol. XVI, Art. IV, Feb., 1927, p. 249. *New synonymy*.

Female.—Length 6.5–8 mm. Head black with the clypeus entirely or partly testaceous, sometimes whitish; thorax mostly black, with the tegulae white, prothorax more or less stained with rufous, femora rufous except extreme apex which is black, base of tibiae sometimes rufescent, abdomen rufous except seventh segment and beyond. Wings hyaline, nervures brown.

Body moderately densely hairy. Head very finely punctured, clothed with conspicuous whitish pubescence below ocelli, vertex minutely punctured, shining and robust; eyes quite deeply emarginate, malar space scarcely one-half length of first antennal segment; postocular area shorter than eye, seen from above, almost as wide, robust and shining, transversely convex, with a minute posterior carina; vertical furrows very deep and wide, two-thirds length of postocellar area; postocellar area quadrate, shining and convex, scarcely raised above level of postocular area; third segment of antenna distinctly longer than fourth, remainder gradually diminishing. Mesonotum very finely and granularly punctured; halves of

anterior lobe gently convex, equally punctured, the lateral areas with a few large distinct pits; lateral lobes minutely punctured; post-tergite triangular or sub-crescentic, smooth, with or without a median carina; meso-episternum with many large smooth punctures, mostly not touching each other but well separated; pectus shining, minutely punctured, diagonal row represented by scattered large pits; claws with a small tooth (Figure 12). Sheath (Figure 8) nearly twice as long as wide; dorsal margin straight or slightly convex, ventral margin evenly rounded; angle sharp; setae fairly long, fine and thick, the longest occurring just below tip; cerci not attaining half length of sheath. Saw as in Figure 5, long and slender, somewhat suggestive of *elderi*; lance serrate; lancet with distinct lobes, minutely toothed, spurette the last pimple-like tooth of lobe; alae reduced to alar spines and a conspicuous alar spur which might be confused with the spurette, alar spur distinct and separate from the reduced alae.

Male.—Similar in size, color and structure to female, differing as follows: clypeus and face below antennae whitish-rufous; hypopygium fairly long, slender, sides of apex distinctly concave near tip, posterior margin narrow, roundly truncate. Genitalia as for subgenus (Figure 64).

Neotype.—♀, Seymour, Illinois, May 1, 1929 (H. H. Ross). Deposited in the collection of the Illinois State Natural History Survey, Urbana, Illinois.

Distribution.—COLORADO: 1 ♀, Colo. CONNECTICUT: Quilford, Hartford, Durham. June. ILLINOIS: Urbana, White Heath, Seymour, St. Joseph, Champaign, Chicago, Algonquin, Elizabeth, Savanna, Rock Island, Ogden, Glencoe, Muncie, Waukegan, Garden City, Grand Detour and Springfield, April to July. INDIANA: Hessville. April and May. IOWA: Ames, Mt. Pleasant. May and June. MAINE: Eagle Bend, Orono. July. MARYLAND: 1 ♀, Md. MASSACHUSETTS: Springfield, Boston, Chicopee. May. MICHIGAN: Douglas Lake, Ann Arbor, Charlevoix. July. MINNESOTA: Foley, Northfield, St. Cloud, Milaca, Moore Lake, Fairbault County, Hennepin County. June to August. MONTANA: 1 ♂, Mon. NEBRASKA: Ashland, Sowbelly Cañon (Sioux County). June. NEW HAMPSHIRE: Franconia. NEW JERSEY: Bergen County, Caldwell, Ramsey, Elizabeth. June and July. NEW YORK: Ithaca, Plattsburg, Rouses Point, Utica, Richfield Springs, White Plains, Brooklyn, Niagara Falls, Staten Island, New York City, Carolina, Dryden Lake, Albany, Newport, Karner, Speculator, Cedar Hills, Meadowlake, Axton, McLean, Victor. May to July. OHIO: Columbus, Norwalk, Sandusky, Salineville. May and June. PENNSYLVANIA: Edge Hill, Harrisburg, Montgomery County. June. SOUTH DAKOTA: Brookings, Elk's Point. June. TEXAS: 1 ♂, Tex. VIRGINIA: Great Falls. WASHINGTON: 1 ♀, Olympia, June 6, 1892. WISCONSIN: 1 ♀, Madison. July. MONTANA: Aweme, Treesbank, Birtle. June. NEW

BRUNSWICK: Bathurst. July. ONTARIO: Ottawa, Bonville, Vineland. May and June. QUEBEC: St. John's County, Montreal, Hull, Hemmingford, Megantic, Lanoraie, Fairy Lake, Rouville, St. Hilaire, Chamby County, Shawbridge. May to July.

A widely distributed species, apparently common in the northern, eastern and central United States and southeastern Canada.

In the vicinity of Urbana this species appears later in the season than any other member of the genus, occurring very abundantly in late May and during June in the Equisetum—Carex communities along the railroads. Its peak comes some two or three weeks after *similis* is on the wane, and forms the last of a well marked series of abundance peaks of different species in the genus.

This species can be readily distinguished from *acidus* and *albifrons* by the circular punctures of the pleurae, and from *napeus* by the red color of the femora, abdomen, etc.

Dolerus apricus var. *alticinctus* MacGillivray

Loderus alticinctus MacGillivray, Univ. Ill. Bull., Vol. XX, No. 50, Aug. 13, 1923, p. 20; Frison, Bull. Ill. Nat. Hist. Surv., Vol. XVI, Art. IV, Feb., 1927, p. 249.

Loderus ancisus MacGillivray, Univ. Ill. Bull., Vol. XX, No. 50, Aug. 13, 1923, p. 21; Frison, Bull. Ill. Nat. Hist. Surv., Vol. XVI, Art. IV, Feb., 1927, p. 250. *New synonymy*.

This variety differs from the typical form in having the middle femora almost black, and by being slightly smaller in size. Specimens belonging to this variety are found in small numbers scattered throughout collections of the species from all localities. Every gradation exists between the two forms, hence the variation has held no significance in the present study, and has not been recognized in determinations. It is thought best, however, to retain the name.

Holotype.—♀, Orono, Maine, June 30, 1913. In the MacGillivray Collection, University of Illinois, Urbana, Illinois.

Dolerus napeus MacGillivray

Loderus niger Rohwer, Can. Ent., Vol. XLII, No. 2, Feb., 1910, p. 49. ♂, ♀.

Dolerus napeus MacGillivray, Can. Ent., Vol. LV, No. 3, March, 1923, p. 65. ♀; Frison, Bull. Ill. Nat. Hist. Surv., Vol. XVI, Art. IV, Feb., 1927, p. 241. *New synonymy*.

Dolerus nepotulus MacGillivray, Can. Ent., Vol. LV, No. 3, March, 1923, p. 68. ♂; Frison, Bull. Ill. Nat. Hist. Surv., Vol. XVI, Art. IV, Feb., 1927, p. 243. *New synonymy*.

Dolerus nauticus MacGillivray, Ins. Insc. Mens., Vol. XI, Nos. 1-3, 1923, p. 35. ♀; Frison, Bull. Ill. Nat. Hist. Surv., Vol. XVI, Art. IV, Feb., 1927, p. 242. *New synonymy*.

Female.—Length 7-8 mm. Color entirely black. Wings hyaline.

Structure almost identical with *apricus*, with the following differences: vertex less robust, obliquely narrowed behind eye, not or extremely sparsely punctured, polished; carina along posterior margin small but sharp; post-tergite always with a sharp median carina; claws with small tooth; genitalia identical with *apricus*.

Male.—Same as female except for sexual differences.

Holotype.—♀, Mts. near Claremont, California. In the U. S. National Museum, Washington, D. C.

Allotype.—♂, same data. Deposited with holotype.

Distribution.—CALIFORNIA: many males and females, Mts. near Claremont, Stanford University, Corte Madero Creek Cañon, Redwood Canyon, Sierrro Nevada, Felton, St. Cruz Mts., Berkeley. Taken from March to May. OREGON: Ore., Corvallis, Drift Creek. April and May. WASHINGTON: Pullman. April.

A species confined to the states of the Pacific Coast, quite rare in collections. It is distinguished from all other members of the subgenus by its black color.

The placing of *Loderus* as a subgenus of *Dolerus* brings the name *niger* Rohwer (1910) into competition with *Dolerus niger* (Linn.) (1767). The name proposed by Rohwer must therefore fall. MacGillivray in 1923 described a species of *Dolerus* giving it the name *napaeus*. Since this is a synonym of *Loderus niger* Rohwer, the name *napaeus* is herein substituted for *niger* (Rohwer), now a preoccupied name.

Dolerus albifrons (Norton)

Dosytheus apricus var. *albifrons* Norton, Proc. Bost. Soc. Nat. Hist., Vol. VIII, 1861, p. 152.

Dolerus albifrons Norton, Trans. Amer. Ent. Soc., Vol. I, 1867, p. 237; Provancher, Addit.

Faun. Can., Hym., 1885, p. 7; Dalla Torre, Cat. Hymen., Vol. I, 1894, p. 2.

Dolerus minusculus MacGillivray, Can. Ent., Vol. XL, No. 4, April, 1908, p. 127; Frison,

Bull. Ill. Nat. Hist. Surv., Vol. XVI, Art. IV, Feb., 1927, p. 241. *New synonymy*.

Loderus accuratus MacGillivray, Univ. Ill. Bull., Vol. XX, No. 50, Aug. 13, 1923, p. 19;

Frison, Bull. Ill. Nat. Hist. Surv., Vol. XVI, Art. IV, Feb., 1927, p. 249. *New synonymy*.

Female.—Length 6 mm. Head mostly black, with the labrum white, clypeus, base of mandibles, and extreme base of first antennal segment rufous; thorax black with the tegulae and base of tibiae white, trochanters and legs otherwise rufous except black ring at apex of posterior femora, and tibiae and tarsi which are more or less brownish-infusate; abdomen rufous with the seventh segment and beyond black. Wings hyaline.

Head below vertex minutely densely reticulate; vertex more or less shining, minutely punctured; eyes not so long as in *apricus*, but evenly emarginate, malar space slightly longer than half basal segment of antenna; postocular area robust and shining, not as long as eye, seen from above, with the posterior carina barely indicated; vertical furrows short, comma-like; postocellar area flat, nearly twice as wide as long, reticular-punctate; third antennal segment subequal to fourth. Halves of anterior lobe uniformly convex; anterior lobe finely reticularly punctured, less roughly on disk than on sides; lateral lobes dull, closely, finely punctured; post-tergite sharply triangular, polished, with a tent-shaped median carina; meso-episternum very slightly depressed above pectus, extremely finely and

roughly reticulate; pectus shining, but with very dense small punctures; tarsal claws without a tooth (Figure 11). Sheath as in Figure 10, very little longer than wide, dorsal margin straight, ventral margin arcuately rounded, lateral surface slightly bulbous near tip, with a distinct carina adjacent to dorsal margin, nearly reaching tip; setae fine, in an evenly graded series; cerci short, attaining only half dorsal length of sheath. Saw very long and slender, slightly upturned at tip (Figure 6); lance almost without serrations; lancet with very faintly indicated armature, lobes barely indicated, minutely toothed, spurettes unrecognizable, undoubtedly fused with lobes, alae represented by a row of minute spines, alar spurs very small and triangular, distinctly connected with the row of alar spines; ventral spines obsolete.

Male.—Similar in size, color and structure to female, with the following differences: labrum, clypeus and spot below bases of antennae, white; hypopygium narrow at apex, sides almost straight, posterior margin truncate; genitalia as for *apricus*, differing only in having the apices of the praetium slightly more prolonged and narrower.

Lectotype.—♀, Connecticut. Designated in manuscript by Rohwer, October, 1920. Deposited in the collection of the Yale University Museum, New Haven, Connecticut.

Lectoallotype.—♂, Connecticut. Designated by Rohwer at the same time and place, and deposited with lectotype.

Distribution.—CALIFORNIA: 1♂, 3♀, Redwood Canyon, Marin County, May 17, 1908. CONNECTICUT: 2♂♂, 1♀, Conn.; ILLINOIS: 1♂, Algonquin (Nason), 1♂, Ill.; 46♂♂, 68♀♀, Fox Lake, May 15, 1930 (Frison and Ross). IOWA: 1♀, Mt. Pleasant, May 23, 1928 (W. Lee). MAINE: 1♀, Orono, June 12, 1913. NEBRASKA: 1♀, Ashland; NEW YORK: 1♂, McLean, May 31, 1898; 1♀, Ithaca, May 31, 1891. ONTARIO: 1♀, Hull, June 9, 1884; 1♀, Bonville, June 24, 1913 (W. A. Ross); QUEBEC: 1♀, Shawbridge, May 28, 1922 (J. W. Buckle).

A rare species of wide distribution. Easily distinguished from *apricus* in lacking a tooth on the tarsal claws and in having the pleurae finely reticulate; and from *acidus* by the small rounded sheath (Figure 10).

Dolerus acidus (MacGillivray)

Dolerus acidus MacGillivray, Univ. Ill. Bull., Vol. XX, No. 50, Aug. 13, 1923, p. 20; Frison' Bull. Ill. Nat. Hist. Surv., Vol. XVI, Art. IV, Feb., 1927, p. 249.

Female.—Length 7–7.5 mm. Head black with the labrum and vague lateral areas on the clypeus rufous; thorax black with the tegulae white, the prothorax, sides of anterior lobe and sometimes faint spots on the lateral lobes and pleurae, rufous; apices of coxae, femora entirely and base of tibiae rufous, rest of tibiae and tarsi blackish-brown; abdomen rufous with more or less of seventh or eighth and following segment, and sheath

black. Front and middle femora sometimes with basal half black or blackish, shading into rufous towards apex. Wings hyaline.

Punctuation of head and thorax much as in *albifrons*. Head below vertex finely and densely reticulate; postocular area only half length of eye. seen from above, narrowed behind eye, densely punctate, dull, with a distinct posterior carina; vertical furrows obsolete, represented by a faint line; postocellar area confluent with postocular area, reticulate; third segment of antenna about a fourth longer than fourth, remainder practically subequal. Anterior lobe very gently convex, dull with dense punctures; lateral lobes densely punctate but with moderately large punctures; posttergite triangular, distinctly striate, with a gentle median carina; mesoepisternum densely and finely reticulate as in *albifrons*; pectus with dense punctures; tarsal claws with or without a small tooth. Sheath very large, as in Figure 9, the ventral margin straight, the dorsal margin arcuately rounded, the two forming a distinct small hook on the caudo-ventral corner; setae fine, almost equal in length; cerci very small, about one-fourth dorsal length of sheath. Saw extremely aberrant in appearance, short and stocky, curved downward (Figure 4); lance regular, not serrate; lancet well armed, lobes distinct, minutely toothed, spurettes small but distinct and separate just within ventral margin, alae almost entirely cut into somewhat irregular alar and ventral spines, and with a long, slightly-upcurved, finger-like alar spur, situated within the dorsal half of the lancet.

Male.—Similar in size, color and structure to female, differing as follows: clypeus less vaguely marked with white, the white showing as two distinct spots one on each side of the meson; entire dorsum of thorax black except rufous posterior margin of pronotum; tibiae not blackish-infusate but more rufous-brown on basal half; hypopygium wider than in *albifrons*, the posterior margin slightly convex; genitalia as for *albifrons*.

Holotype.—♀, Orono, Maine, June 12, 1913. In the MacGillivray Collection, University of Illinois, Urbana, Illinois.

Allotype.—♂, Canada (C. F. Baker). Also in the MacGillivray Collection. (Present Designation).

Distribution.—ILLINOIS: 5 ♀ ♀, Algonquin, May 4 to 21, 1895 (Nason); 1 ♀, Starved Rock, 16 ♂ ♂, 5 ♀ ♀, Waukegan, 2 ♀ ♀, Dixon, 1 ♂, 4 ♀ ♀, Garden City and 2 ♂ ♂, 18 ♀ ♀, Grand, Detour May 13-16, 1930 (Frison and Ross). MAINE: 1 ♀, Orono, June 12, 1913. NEW YORK: 2 ♀ ♀, Ithaca; 3 ♀ ♀, Albany, May 22, 1903; 3 ♂ ♂, Newport, May 26, 1902; 1 ♂, Lancaster, May, 1886; 1 ♂, Chatham, August 19, 1904. PENNSYLVANIA: 2 ♀ ♀, Edge Hill, May 20, 1900. QUEBEC: 3 ♀ ♀, Lano-raie, June 18, 1915 (Beaulieu).

Another rare species, like the preceding. Easily recognized by the finely reticulate pleurae and the curious, large sheath with the "hook" (Figure 9).

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PLATE I

EXPLANATION OF PLATE I

- FIG. 1. Lateral view of abdomen of *D. illini*.
 FIG. 2. Lateral view of hypothetical saw.
 FIG. 3. Lateral view of saw of *D. neoaprilis*.
 FIG. 4. Lateral view of saw of *D. acidus*.
 FIG. 5. Lateral view of saw of *D. apricus*.
 FIG. 6. Lateral view of saw of *D. albifrons*.
 FIG. 7. Ventral view of abdomen of *D. similis*.
 FIG. 8. Lateral view of sheath of *D. apricus*.
 FIG. 9. Lateral view of sheath of *D. acidus*.
 FIG. 10. Lateral view of sheath of *D. albifrons*.
 FIG. 11. Tarsal claw of *D. albifrons*.
 FIG. 12. Tarsal claw of *D. acidus*.
 FIG. 13. Tarsal claw of *D. agcistus*.
 FIG. 14. Tarsal claw of *D. bicolor*.
 FIG. 15. Cephalic view of eye of subgenus *Dolerus* Jur.
 FIG. 16. Cephalic view of eye of subgenus *Loderus* Kon.

ABBREVIATIONS USED

<i>a</i> = ala	<i>lb</i> = lobe
<i>ac</i> = alar spines	<i>ln</i> = lance
<i>ad</i> = alar spur	<i>lt</i> = lancet
<i>b</i> = annuli	<i>s</i> = sternite
<i>c</i> = cercus	<i>sh</i> = sheath
<i>d</i> = tooth or <i>dens</i>	<i>sp</i> = spiracle
<i>hy</i> = hypopygium	<i>sr</i> = spurette
<i>j</i> = base of sheath	<i>t</i> = tergite
<i>x</i> = ventral spines	

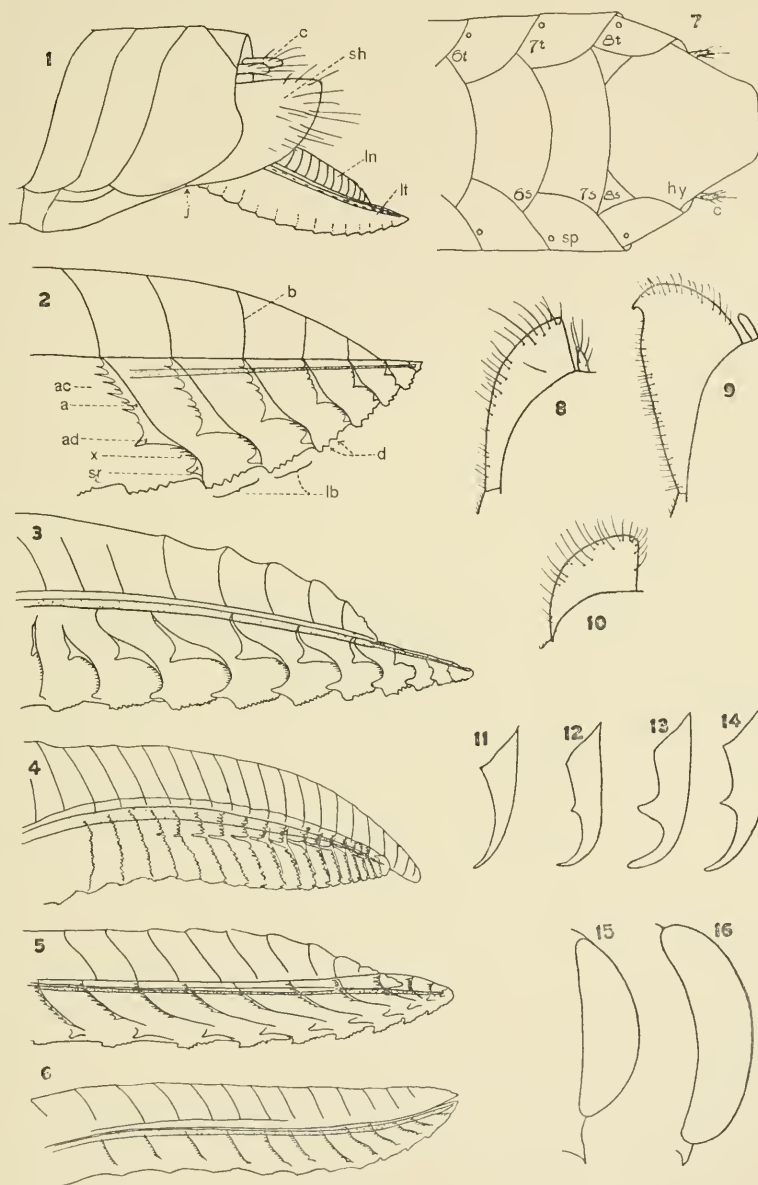


PLATE II

EXPLANATION OF PLATE II

- FIG. 17. Lateral view of sheath of *D. tectus*.
FIG. 18. Lateral view of sheath of *D. sericeus* subsp. *neosericeus*.
FIG. 19. Lateral view of sheath of *D. sericeus* subsp. *centralis*.
FIG. 20. Lateral view of sheath of *D. sericeus* subsp. *parasericeus*.
FIG. 21. Lateral view of sheath of *D. sericeus*.
FIG. 22. Lateral view of sheath of *D. unicolor*.
FIG. 23. Lateral view of sheath of *D. illini*.
FIG. 24. Lateral view of sheath of *D. borealis*.
FIG. 25. Lateral view of sheath of *D. versa*.
FIG. 26. Lateral view of sheath of *D. nortoni*.
FIG. 27. Lateral view of sheath of *D. collaris*.
FIG. 28. Posterior-lateral view of sheath of *D. collaris*.
FIG. 29. Lateral view of sheath of *D. bicolor*.
FIG. 30. Posterior-lateral view of sheath of *D. neogcistus*.
FIG. 31. Posterior-lateral view of sheath of *D. interjectus*.
FIG. 32. Posterior-lateral view of sheath of *D. distinctus*.
FIG. 33. Lateral view of sheath of *D. similis* (short type).
FIG. 34. Lateral view of sheath of *D. nicaeus*.
FIG. 35. Lateral view of sheath of *D. nasutus*.
FIG. 36. Lateral view of sheath of *D. neoaprilis*.
FIG. 37. Lateral view of sheath of *D. similis* subsp. *nescius*.
FIG. 38. Lateral view of sheath of *D. similis* (*plesius*, or long, type).
FIG. 39. Lateral view of sheath of *D. aprilis*.
FIG. 40. Lateral view of sheath of *D. elderi*.



PLATE III

EXPLANATION OF PLATE III

- FIG. 41. Apical portion of saw of *D. unicolor*.
FIG. 42. Ventral margin of saw of *D. unicolor*.
FIG. 43. Ventral margin of saw of *D. borealis*.
FIG. 44. Saw of *D. illini*.
FIG. 45. Ventral margin of saw of *D. illini*.
FIG. 46. Ventral margin of saw of *D. parasericeus*.
FIG. 47. Lancet of *D. neosericeus*.
FIG. 48. Lancet of *D. versa*.
FIG. 49. Saw of *D. clypealis*.
FIG. 50. Lancet of *D. collaris*.
FIG. 51. Ventral margin of saw of *D. nortoni*.
FIG. 52. Lancet of *D. neoagcistus*.
FIG. 53. Lancet of *D. bicolor*.
FIG. 54. Lancet of *D. agcistus*.
FIG. 55. Lance of *D. abdominalis*.
FIG. 56. Lance of *D. interjectus*.
FIG. 57. Saw of *D. elderi*.
FIG. 58. Lancet of *D. nasutus*.
FIG. 59. Lancet of *D. similis*.
FIG. 60. Lancet of *D. tejoniensis*.
FIG. 61. Saw of *D. piercei*.

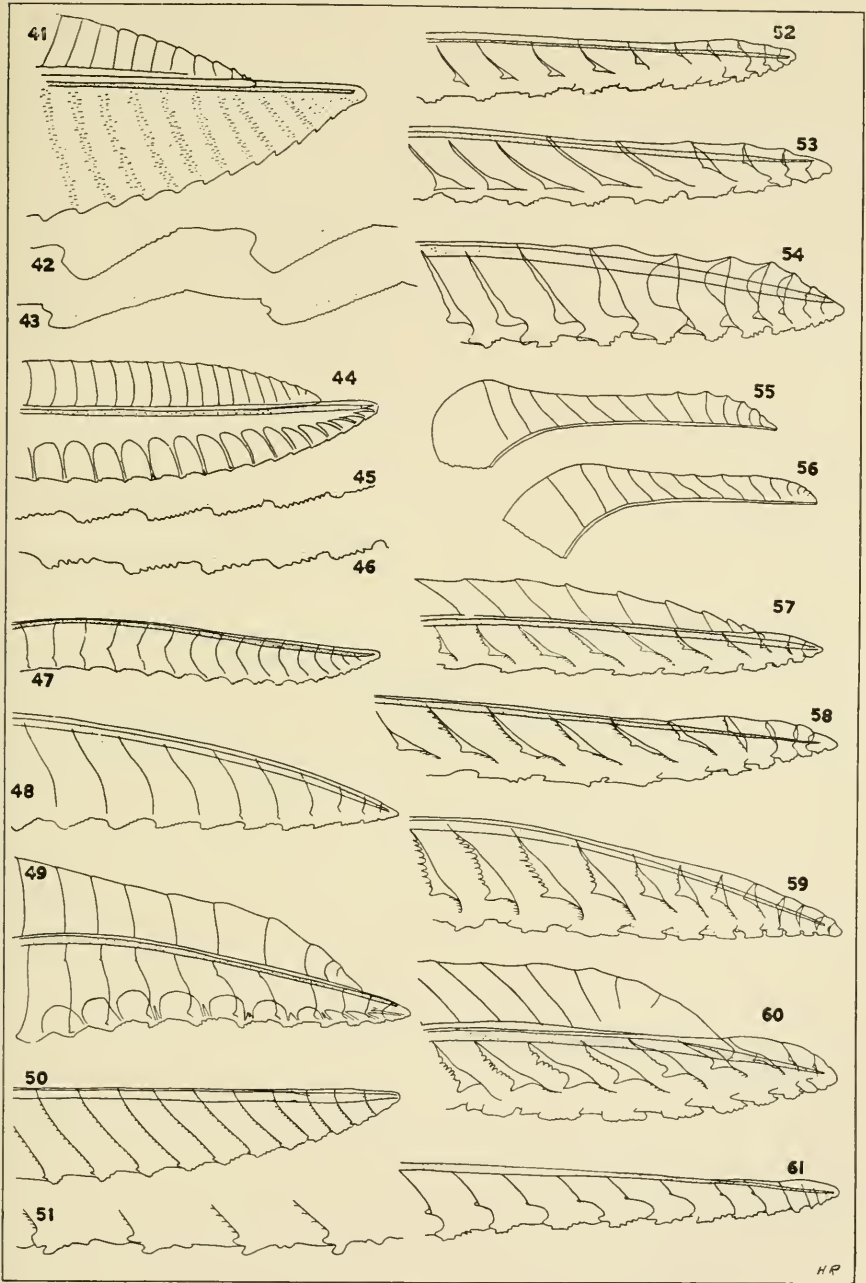


PLATE IV

EXPLANATION OF PLATE IV

- FIG. 62. Dorsal view of head of *D. elderi*.
 FIG. 63. Dorsal view of thorax of *D. elderi*.
 FIG. 64. Ventral view of male genitalia of *D. acidus*.
 FIG. 65. Ventral view of male genitalia of *D. unicolor*.
 FIG. 66. Ventral view of male genitalia of *D. sericeus* race *centralis*.
 FIG. 67. Ventral view of male genitalia of *D. agcistus*.
 FIG. 68. Ventral view of male genitalia of *D. similis*.
 FIG. 69. Ventral view of male genitalia of *D. frisoni*.

ABBREVIATIONS USED

<i>al</i> = anterior lobe, dextral half	<i>p</i> = penis rods
<i>cl</i> = clypeux	<i>pc</i> = postocular area
<i>f</i> = vertical furrows	<i>po</i> = postocellar area
<i>g</i> = gonocardo	<i>pp</i> = praeputium
<i>h</i> = harpes	<i>pr</i> = pronotum
<i>ll</i> = lateral lobe	<i>px</i> = post-tergite
<i>m</i> = membrane of wing	<i>sc</i> = scutellum
<i>oc</i> = ocellar basin	<i>sl</i> = gonostipes
	<i>v</i> = penis valves

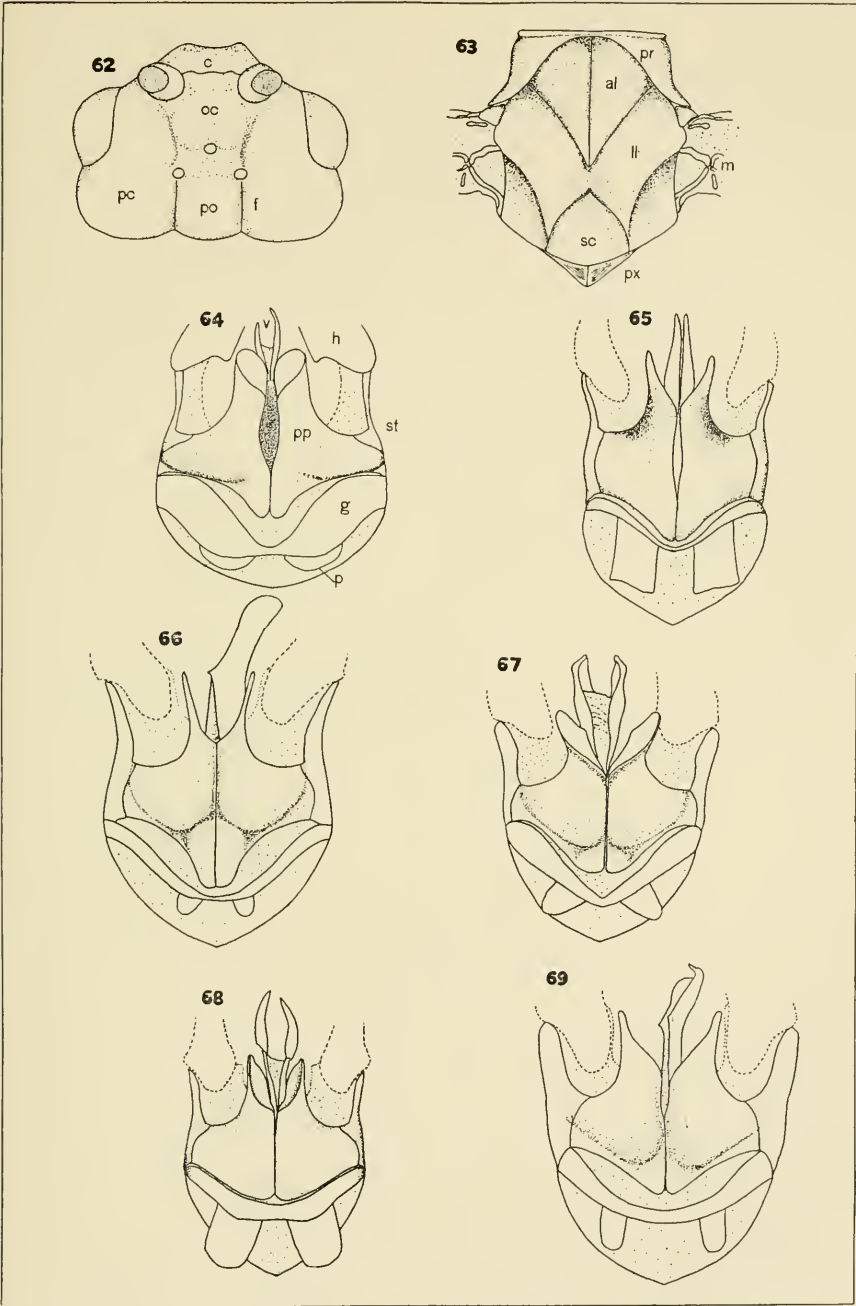


PLATE V

EXPLANATION OF PLATE V

FIG. 70. Front and hind wings of *Dolerus similis* (Nort.).

FIG. 71. Seasonal abundance of the commoner species of *Dolerus* at the Seymour habitat in 1929: 1, *D. agcistus*; 2, *D. illini*; 3, *D. aprilis*; 4, *D. similis*; 5, *D. apricus*.

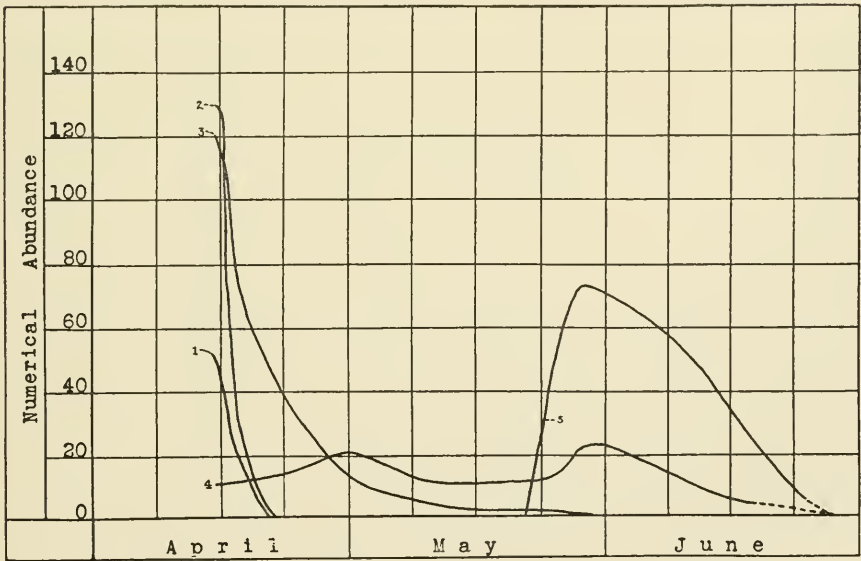
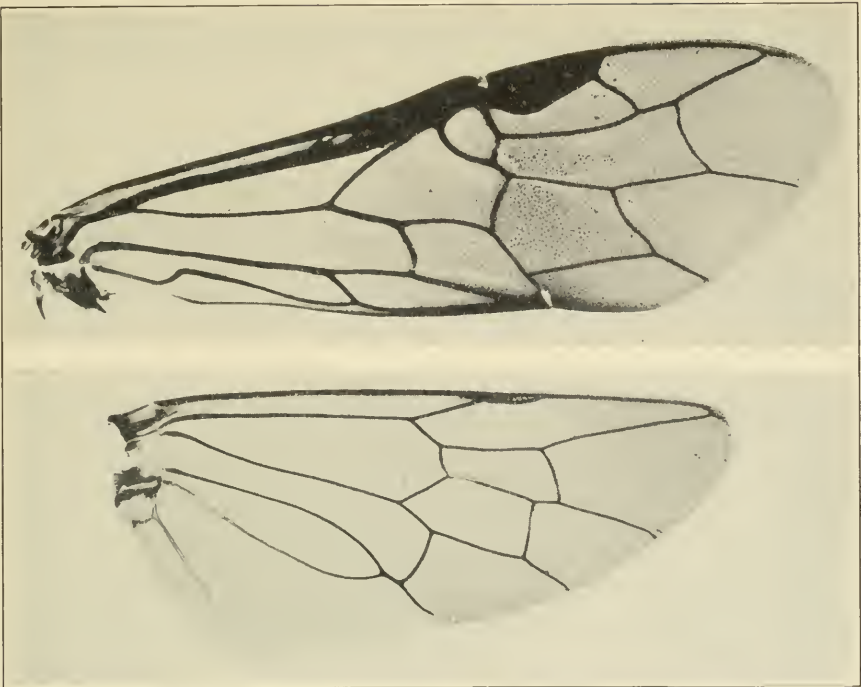


PLATE VI

EXPLANATION OF PLATE VI

- FIG. 72. *Dolerus* habitat along railroad tracks, Seymour, Illinois, April 20, 1929. *Equisetum*-*Carex* community.
- FIG. 73. *Dolerus* habitat along railroad tracks, Savoy, Illinois, April 20, 1929. *Equisetum* community.



INDEX

The names of all species, sub-species, and varieties are here listed under the four generic names, *Dolerus*, *Dosytheus*, *Loderus*, and *Tenthredo*. Those reduced to synonymy are indicated by *italic* type, and new names by **bold-face** type.

- Dolerides*, 24
Dolerinae, 24
Dolerini, 24
Dolerus Guillebeau, 26
Dolerus Jurine, 24, 25
 abdominalis (Norton), 29, 30, 66
 acidus (MacGillivray), 93, 97
 acritus MacGillivray, 77
 agcistus MacGillivray, 16, 18, 29, 31, 59
 var. *maroa* new variety, 29, 61
 albifrons (Norton), 93, 96
 alticinctus MacGillivray, 95
 apricus (Norton), 15, 16, 17, 19, 93
 var. *alticinctus* MacGillivray, 93, 95
 aprilis (Norton), 15, 16, 17, 18, 30, 32, 84
 var. *nocivus* MacGillivray, 30, 85
 apriloides MacGillivray, 30, 32, 72
 arvensis Say, 36
 auraneus new variety, 69
 bicolor (Beauvois), 22, 29, 31, 58
 var. *lesticus* MacG., 28, 59
 var. *nigrita* new variety, 28, 59
 borealis MacGillivray, 27, 38
 centralis new subspecies, 46
 coccinifera Norton, 87
 coccinifer Dalla Torre, 87
 cohaesus MacGillivray, 67
 collaris Say, 13, 18, 22, 28, 31, 53
 var. *erebus* new variety, 28, 55
 var. *icterus* MacGillivray, 29, 56
 var. *maculicollis* (Norton), 29, 55
 coloradensis Cresson, 28, 31, 86
 colosericeus MacGillivray, 44
 conjectus new variety, 80
 conjugatus MacGillivray, 77
 coruscans Konow, 14
 clypealis new species, 29, 50
 var. *nigrilabris* new variety, 29, 51
 distinctus Norton, 29, 61
 dubius Klug, 21
 dysporus MacGillivray, 84
 eglanteriae Klug, 25
 elderi Kincaid, 30, 32, 67
 var. *auraneus* new variety, 30, 32, 69
 var. *melanus* new variety, 28, 31, 70
 var. *rubicanus* new variety, 30, 32, 70
 erebus new variety, 55
 eurybis new species, 29, 30, 65
 femur-rubrum Rohwer, 93
 frisoni new species, 32, 91
 fumatus new subspecies, 81
 germanica Fabricius, 24
 gibbosus Hartig, 14
 gonagra Fabricius, 14, 22, 24, 26
 graenicheri MacGillivray, 59
 haematodes Schrank, 14, 22
 icterus MacGillivray, 56
 idahoensis new species, 28, 63
 illini new species, 16, 18, 27, 31, 39
 var. *rufilobus* new variety, 31, 41
 inspectus MacGillivray, 77
 inspiratus MacGillivray, 77
 interjectus new species, 29, 32, 63
 konowi MacGillivray, 90
 lesticus MacGillivray, 59
 luctatus MacGillivray, 93
 maculicollis (Norton), 55
 madidus Klug, 14, 22
 maroa new variety, 61
 melanus new variety, 70
 minusculeus MacGillivray, 96
 monosericeus MacGillivray, 44
 moramus new species, 29, 30, 62
 napaeus MacGillivray, 93, 95
 narratus MacGillivray, 35
 nasutus MacGillivray, 28, 31, 71
 nativus, MacGillivray, 32, 38
 nauticus MacGillivray, 95
 necessarius MacGillivray, 83
 nectareus MacGillivray, 38
 neosericeus MacGillivray, 47
 nefastus MacGillivray, 77
 memorosus MacGillivray, 67
 neoagcistus, MacGillivray, 13, 15, 17, 18,
 29, 31, 56
 neoprilis MacGillivray, 18, 21, 30, 32, 88
 subsp. *konowi* MacGillivray, 28, 31, 90
 neocollaris MacGillivray, 27, 31, 33
 subsp. *narratus* MacGillivray, 27, 31, 35
 neosericeus MacGillivray, 47
 neostugnus MacGillivray, 57
 nepotulus MacGillivray, 95

Dolerus Jurine (continued)

- nervosus* MacGillivray, 80
nescius MacGillivray, 82
nicaeus MacGillivray, 22, 28, 31, 83
nidulus MacGillivray, 90
nigratus Müller, 14, 22
nigrilabris new variety, 51
nigrita new variety, 59
nigritella new variety, 53
nimbosus MacGillivray, 83
nivatus MacGillivray, 88
nocivus MacGillivray, 85
nocuus MacGillivray, 35
nominalus MacGillivray, 38
nordanus new subspecies, 80
nortoni new species, 17, 29, 31, 51
 var. *nigritella* new variety, 28, 53
novellus MacGillivray, 71
novicius MacGillivray, 78
nugatorius MacGillivray, 71
numerosus MacGillivray, 90
nummarius MacGillivray, 79
nummatus MacGillivray, 77
nundinus MacGillivray, 74
nuntius MacGillivray, 74
nutricius MacGillivray, 67
nyctelius MacGillivray, 67
palustris (Klug), 14, 22
parasericeus MacGillivray, 45
pedestris Panzer, 24
piercei Rohwer, 29, 49
plesius MacGillivray, 77
polysericeus MacGillivray, 45
pratensis Linnaeus, 14, 22, 24, 25
refugus MacGillivray, 33
rubicanus new variety, 70
rufilobus new variety, 41
sericeus Say, 27, 31, 43, 44
 subsp. *centralis* new subsp., 43, 44, 46
 subsp. *neosericeus* MacGillivray, 43, 44, 47
 subsp. *parasericeus* MacGillivray, 43, 44, 45
similis (Norton), 13, 15, 16, 17, 19, 22, 30, 32, 75, 76, 77
 subsp. *fumatus* new subspecies, 75, 76, 81
 subsp. *nescius* MacGillivray, 75, 76, 82
 subsp. *nordanus* new subspecies, 76, 80
 subsp. *simulans* Rohwer, 75, 76, 81
 var. *conjectus* new variety, 75, 76, 80
 var. *novicius* MacGillivray, 76, 78
 var. *nummarius* MacGillivray, 76, 79
 var. *tibialis* Cressen, 75, 76, 80
 var. *yukonensis* Norton, 74
simulans Rohwer, 81
 sp. 2 Yuasa, 17
stagnus MacGillivray, 77
tectus MacGillivray, 27, 31, 41
tejonensis (Norton), 28, 30, 87
tejonensis Weldon, 86
thoracicus Kirby, 36
thoracinus Beauvois, 36
tibialis Cressen, 80
unicolor (Beauvois), 13, 15, 17, 18, 22, 27, 30, 35
 versa Norton, 29, 30, 48
 yukonensis Norton, 30, 32, 74
Dosyltheus, 25, 92
 abdominalis Norton, 66
 apricus Norton, 84, 93
 var. *albifrons* Norton, 96
 aprilis Norton, 84
 bicolor Norton, 58
 maculicollis Norton, 55
 similis Norton, 77
 tejonensis Norton, 87
Loderus Konow, 21, 25, 92
 accuratus MacGillivray, 96
 acerbus MacGillivray, 93
 acidus MacGillivray, 97
 acriculus MacGillivray, 67
 albifrons MacGillivray, 93
 alticinctus MacGillivray, 95
 ancisus MacGillivray, 95
 niger Rohwer, 95
Tenthredo *bicolor* Beauvois, 58
 collaris Donovan, 55
 pratorum Fallen, 92
 thoracinus Beauvois, 35
 unicolor Beauvois, 35

ILLINOIS BIOLOGICAL MONOGRAPHS

Vol. XII

No. 4

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A STUDY OF FRESH-WATER PLANKTON
COMMUNITIES

WITH NINE FIGURES

BY
SAMUEL EDDY

CONTRIBUTION FROM THE ZOOLOGICAL LABORATORY OF THE
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CONTENTS

	PAGE
Introduction.	7
Areas Studied	11
Methods.	11
Constitution of the Plankton in Streams	13
Stable Streams	13
Impounded Streams.	17
Young Streams	19
Constitution of the Plankton in Lakes and Ponds	22
Shallow Lakes and Perennial Ponds	23
Temporary Ponds	26
Deep Glacial Lakes	29
Seasonal Communities as Indicated by Plankton Organisms	37
Stable Streams and Perennial Ponds	37
Young Streams	45
Temporary Ponds	45
Glacial Lakes.	46
Plankton Development and Related Factors	47
Age of Water.	48
Temperature	51
Velocity and Water Level	52
Turbidity	53
Light	53
Chemical Factors	54
Biological Factors	55
Interrelations of Factors	56
Geographical Distribution and Ecological Classification	57
Summary	61
Check List of Names of Species	63
Tables	65
Bibliography	87
Index.	91

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INTRODUCTION

Various ecologists have frequently demonstrated that both plants and animals exist on land in well-defined communities, but have given comparatively little attention to the existence and character of similar communities in water. Land communities show definite development and behavior. Certain species known as "predominants" (Smith, 1928), or "prevalents," are conspicuous in land communities because of their size or because of their abundance due to a favorable response to the conditions and they serve as an index to the community. Some of them have approximately the same abundance throughout the year, while others show seasonal fluctuations in abundance and indicate the presence of seasonal societies or "socies" (Clements, 1916). Some predominants, known as "euryoecious" species, have such widespread distribution as to mark the boundaries of the formation, which is the community of greatest rank. Others of limited distribution are termed "stenoecious" and indicate the boundaries of communities of associational rank.

Land communities develop and reach maturity by a long series of successional stages. If comparable fresh-water communities exist, they may be expected to reach maturity through a series of developmental stages. Communities of various ranks comparable to similar aggregations on land should be definitely ascertainable in fresh water. It should be possible to show a series of developmental communities ultimately reaching a permanent stable condition equivalent to that of a terrestrial climax community, as outlined by plant ecologists (Clements, 1916).

Most ecologists have assumed that permanent fresh-water communities do not exist and that aquatic communities are but early developmental stages of terrestrial ones. The writer believes that permanent fresh-water communities exist, reach maturity, and show aspects comparable to terrestrial communities (Shelford and Eddy, 1929).

Aquatic communities should demonstrate their stability and permanence by maintaining a composition in which no further succession takes place. Their rank and status should be determined by the presence of predominant or dominant organisms. It is part of the purpose of this paper, by studying plankton as an index to the pelagic portion of fresh-water communities, to determine the existence, rank, behavior, and status of the plankton element.

"Plankton" has been variously defined by many authorities. Hensen (1887) originally defined the term as denoting all that floats in water, "Alles was in Wasser treibt." Kolkwitz (1912) defined the term as the natural community of those organisms that are normally living in water

and are passively carried along by currents. Rylov (1922) in discussing the forms which come under the term plankton, uses the terms "obligoplankton," referring to true planktonts only, and "facultative planktonts," referring to those forms found in both limnetic and littoral regions, and also states that "pelagic organisms" are not the same as "planktonts," for planktonts may be both pelagic and littoral. Plankton investigators usually include under the term all forms found in open waters regardless of origin; consequently, they often include many bottom and shore forms. As the term is restricted to minute forms and does not include the larger organisms such as fishes, the writer regards the term as applied to an aggregation of organisms constituting all microscopic forms found in open waters. Properly speaking, although seldom recognized as such, bacteria living in open waters should be included under the term "plankton." A common definition includes those forms with little or no resistance to currents, living a free-floating or suspended existence in open or pelagic waters.

Kolkwitz and Marsson (1902, 1908, 1909) have attempted to classify plankton from the standpoint of pollution, using plankton organisms as indicators of degrees of pollution. Wesenberg-Lund (1908), Bachmann (1921), Smith (1920), Naumann (1927), and Krieger (1927) all have attempted to classify plankton in terms of plankton constituents and relations to the habitats. Griffith (1923) has classified plankton algae in terms of the ecological features prevalent in the habitat. From such attempts have arisen such terms as "rheoplankton" (river), "benthoplankton" (shallow pond), "limnoplankton" (deep pond), "heleoplankton" (pond), and many others, all describing the plankton on the basis of habitats. The writer realizes that all these types of plankton are distinct and can be distinguished from each other by their specific composition but believes that they should be classified on the basis of the abundant or conspicuous organisms which act as indicators because of their favorable response to environmental conditions. A true ecological classification of plankton should recognize plankton as a part of a living community which is comparable to an organic unit passing through the stages of youth and maturity.

The animals of any considerable body of water group themselves into two natural communities, the bottom and the pelagic communities, which may be termed societies or socies as they correspond to the terrestrial stratal societies or socies of Clements (1916). The true community dominants, namely, fishes, do not respect the difference between bottom and open waters. Most fishes are, properly speaking, bottom organisms but their constant forays into open waters place them as important factors in the pelagic community. These socies offer an interrelationship that is unique and entirely different from that of the cor-

responding terrestrial groups. Terrestrial societies all rest on solid substrata, and we know of no group of terrestrial animals which spend their entire existence suspended in the surrounding medium. The organisms of pelagic societies are always suspended in the water. Type of bottom cannot influence the reactions of organisms of the pelagic societies as it does those of the bottom society, which are usually in close contact with the bottom. Furthermore, the pelagic society is constantly shifting with currents or waves, while that of the bottom remains fixed. The development of the pelagic society is not as closely related to, and dependent on, the development of the bottom society, as is the development of the various terrestrial stratal societies to each other. In newly formed bodies of water, as will be discussed later, the pelagic society develops much faster than the bottom society.

The organisms of the plankton constitute an important element in the pelagic community. Over 500 species of organisms have been reported from the plankton of the waters of the State of Illinois. Practically the only other organisms existing in this fresh-water community are the pelagic fishes, which are usually dominants; and in both numbers and species, the plankton organisms greatly out-number these. Truly pelagic or nektonic fishes are rare in fresh waters and are limited to such forms as the cisco and other coregonid fishes which occur only in very deep lakes.

The plankton serves as a convenient index to pelagic communities. Quantitative collections are easily obtained. The great abundance and number of species give a greater range of data than fishes afford. The organisms serve as a good index to general conditions because of their inability to resist currents and to move into more favorable areas; consequently, their abundance may be considered as evidence of favorable reactions to the conditions of the habitat.

In land communities certain species are abundant and therefore conspicuous because of their favorable reactions to environmental conditions and are known as "predominants" or "prevalents." Others, known as "dominants," usually fishes in fresh water, exercise some control over the community and are responsible, in part at least, for its existence. Cahn (1929) found indications that carp introduced into a lake could destroy the vegetation and change the character of the bottom to such an extent as to alter the fish population. Organisms forming important elements in food chains are known as "influents." "Characteristic" organisms are those forms which may serve as indicators of conditions. They are not necessarily abundant; indeed, they are often rather scarce, their mere presence or absence being more significant than their abundance. These terms should be applicable also to fresh-water organisms insofar as communities in water are comparable to those on

land. In this paper we are chiefly concerned with the characteristic and abundant or predominant organisms, which include both seasonals and perennials, as our knowledge and data on interrelations between aquatic organisms are insufficient to determine the other types definitely. Accordingly, all abundant or characteristic species are considered either as perennial predominants ("perennials") or as seasonal predominants ("seasonals") until more is understood about their relations to other members of the community. It is probable that many plankton organisms act as influents by serving as vital elements in the foods of other forms and possibly even as dominants in controlling the community by this action and by clearing up waste and inorganic materials, thus preparing conditions whereby other forms can exist.

Another group of organisms found in the plankton may be termed "incidentals." These forms often constitute more than half of the species but are sporadic and seldom abundant. Such forms generally occur once or twice a year and frequently originate from foreign sources. Therefore, as they are apparently not significant or important to the community, their presence has been generally disregarded in this study and only considered when describing the entire plankton population.

Communities are determined by their organic constitution, in which one or more species stand out and serve as indicators, and by the physiographic state of their habitat. The first analysis of a community should be made from a physiographic study. This is best applied to both permanent and developmental communities. The conception held by most ecologists, that aquatic communities are developmental stages of land communities, is not necessarily true in all cases. Streams are permanent so long as the existing climate endures, and this is the same condition under which land communities reach and maintain a permanent or climax stage. Only the abandoned areas of streams become developmental stages of land communities. Apparently streams contain the only permanent fresh-water communities. Streams show a definite physiographic development, from the small intermittent stream, with its rapid fall, to the large permanent stream approaching a base level and having a uniform current (Shelford, 1913). Their characteristic fluctuations of current and level make it difficult to study their communities.

All lakes are, at least in part, developmental stages of land communities. Physiographically, the ultimate fate of even the deepest lake is to become a swamp proceeding toward a terrestrial climax. Many lakes are enlarged stream channels, forming large and deep bodies of waters. These are best considered as abandoned parts, or natural duplications of abandoned parts, inasmuch as in their later stages, when they proceed toward land, they contain communities similar to stream portions actually abandoned.

AREAS STUDIED

In order to secure the data necessary for the study of plankton as an element of aquatic communities, it was essential to select ponds, lakes, and streams representing all stages of physiographic development. This paper is based on data obtained from more than two thousand collections studied from this viewpoint. Advantage was taken of several dams and canals to furnish quasi-experimental evidence on development and maturity of plankton communities. The most extensive data were obtained from the Sangamon River, a tributary of the Illinois River, between Mahomet and Decatur, Illinois. Collections on this stream were made semi-monthly or weekly at Decatur from 1923 to 1929, at Monticello from 1927 to 1929, and at Mahomet from 1928 to 1929. Collections also were made at stations ten to fifteen miles apart over the entire Rock River system and the Illinois-Mississippi Canal under the direction of the Illinois State Natural History Survey during the summers of 1925, 1926, and 1927. Ponds at Decatur and Urbana were studied semi-monthly from 1926 to 1929. Temporary ponds in the vicinity of Urbana and Seymour, Illinois, were studied weekly during their wet periods in 1926 and 1928. Many occasional collections have been made and studied from various parts of the United States whenever opportunity was afforded to the writer. In addition, extensive collateral data have been obtained from collections made by other workers as follows: by Dr. C. A. Kofoid from the Illinois, Mississippi, and Ohio rivers; by Mr. R. E. Richardson from the Illinois, Mississippi, Ohio, and Fox rivers and from the glacial lakes of northern Illinois; by Dr. S. A. Forbes from lakes of Yellowstone Park and Wisconsin; by Dr. H. J. Van Cleave from lakes of New Mexico, Arizona, and California; by Prof. Frank Smith from lakes in Colorado and Michigan; by Dr. R. D. Bird from lakes in San Juan County, Washington; by Mr. A. L. Hjortland from lakes in Minnesota; by Miss Beth Hefelbauer from lakes in New York; and by Mr. E. E. Wehr from lakes in Montana.

METHODS

The usual methods of collecting by silk net, decantation, filter paper, and centrifuge were employed. Each set of collections consisted of a silk-net collection with an additional collection by one of the other three methods for the purpose of obtaining data on the nanoplankton. At least two samples of each collection were counted in a Sedgwick-Rafter slide, an entire cubic centimeter being counted instead of the usual ten random counts on a single sample. The 200 fields of the microscope on

the slide were divided into ten groups, and the counts of all these groups were made separately and then averaged. From the averages thus obtained on the two samples, the numbers of organisms were finally computed per cubic meter, which was the standard unit volume. This method gave a more representative list of species as well as a better average than is usually secured by the common method of basing computation on a single count of 0.1 cc. It is well known that the silk net is very inefficient and allows many of the smaller organisms to escape through the fine meshes. However, as larger quantities of water could be used (100 liters), it gave better qualitative data than could be obtained by any of the other methods. The quantitative data from the silk net, after repeated tests, showed reasonable accuracy for the larger forms such as the Entomostraca. All the collections referred to in the tables of data in this paper were made with a net of No. 25 bolting silk unless otherwise indicated.

The decantation method proved to be a quite accurate and very convenient method for collecting nanoplankton. A known volume (1000 cc.) of the water was treated with 2 cc. of formalin and allowed to settle for two weeks. The water was carefully siphoned off until only about 20 cc. remained, which was saved with the residue for counting. When floating organisms were present, care was taken not to siphon off any of the surface water. Many of the nanoplankton collections from Lake Decatur and the Sangamon River were of this type. Most of the plankton collections from other waters studied were filter-paper or centrifuge collections.

As plankton organisms are known to vary in vertical distribution, collections were made at several levels in waters where there was little current. By means of either a pump or water bottle, collections were made from two or three levels depending on the depth. Averaging the collections from the different levels served to equalize the variations in vertical distribution. Whenever a current was present and repeated tests had showed no vertical variation, the collections were made either by dipping with a bucket or by pumping a known volume of water from two feet below the surface.

In an effort to find correlations with the distribution of the organisms, the physical conditions of the water were determined as far as possible for each collection taken. At most of the stations tests for dissolved oxygen were made in the various seasons of 1928-29, by the Winkler method (Winkler, 1888) as described by Birge and Juday (1911). The temperature and pH of the water were determined at each collection. Also the level of the water, the turbidity, and the current were noted each time.

Where weekly or semi-monthly collections were made, the data were averaged and tabulated on the monthly basis for convenience. The author is well aware of the many fluctuations in abundance occurring within short periods of even a week, but the long tables necessary to include these detailed data are undesirable because of their additional bulk. Such observations are desirable for a detailed study of plankton, but in a general study monthly averages serve very well.

For each station where series of seasonal collections were made, the organisms have been tabulated in order of abundance or importance and according to their seasonal arrangement, without any regard to their systematic order. This is essential in an ecological paper where distribution is of more importance than systematic relations. As in terrestrial communities, the abundance of organisms is not always the index to their importance. Some very small organisms are very abundant, running into billions per cubic meter, while others much larger are equally important though running only a few hundred per cubic meter.

CONSTITUTION OF THE PLANKTON IN STREAMS

In an ecologically "mature" community there is no change in most of the predominant species from year to year. Such communities should be distinguished from "developmental" communities by their relative stability and by the absence of invaders which would establish different sets of conditions. Communities may be distinguished from others of different status by the presence of abundant or predominant organisms serving as indicators of given sets of conditions.

STABLE STREAMS

Streams for the study of mature communities should be selected first on a physiographical basis. Alterations in the channel, changing the physical or chemical conditions of the water, by an increase in turbidity, by the introduction of water of recent origin, or by an increase in rate of flow, may retard the rate of development or change the ecological age of the water at any given point. The tendency is to wear away the stream bed, creating a more uniform channel. No stream perhaps ever completely reaches the limit of old age, as the upper course is usually in such a physiographic condition as to produce a volume of silt which more or less affects the lower portion. Most of the streams of the United States are in the process of aging, but hardly any two are in the same physiographical stage. Therefore, since the physiographical stages show considerable variation, it is necessary to select those suitable for

the study of the ecological conditions of maturity. The current should be relatively slow and uniform. The Illinois River approaches these conditions very closely. The Mississippi and the Ohio are not as mature as the Illinois. Purdy (1923) states that the Ohio is geologically young, not having reached a base level and being consequently subject to considerable channel erosion. The Mississippi channel is subject to erosion and receives much silt from tributaries; consequently the water is very turbid. Summer collections from Rock Island to Cairo, made by C. A. Kofoed in 1902 and R. E. Richardson in 1908 for the Illinois Natural History Survey, have been examined by the writer and show an abundance of silt and a scanty plankton (Table 1). The same seems to be true of collections by the same investigators from the Ohio between Paducah and Cairo. Galtsoff (1924) in his investigations on the upper Mississippi found the plankton more abundant upstream. He reports a rather general distribution of the following plankton organisms in the section of the river between Hastings, Minnesota, and Alexandria, Missouri: algae, *Microcystis aeruginosa*, *Aphanizomenon flos-aquae*, *Scenedesmus quadricauda*, *Pediastrum duplex*; protozoans, *Eudorina elegans*, *Codonella cratera*; and rotifers, *Filinia longiseta*, *Polyarthra trigla*, *Brachionus calyciflorus*, *Brachionus capsuliflorus* (varieties), and *Keratella cochlearis*. The writer found the plankton to be rather rare both in species and in abundance in the collections of Kofoed and Richardson from the Ohio and the Mississippi. Purdy (1923) gives no definite information as to the specific content of the plankton of the lower Ohio but states that in the Paducah district the plankton is scarce.

The collections made by Richardson from the Ohio and the Mississippi were made continuously by pumping a stream of water through a plankton net suspended in a barrel on deck as the boat traveled down the Mississippi and up the Ohio. In the regions listed in Table 1, little difference existed between the collections within a given region, so that an average of the collections gave a typical and representative list of the plankton for that area. *Diffugia lobostoma* was the most abundant form in the Ohio. The other but less abundant forms were the usual river planktons as follows: *Pediastrum duplex*, *Keratella cochlearis*, *Polyarthra trigla*, *Cyclops viridis*, *Filinia longiseta*, and *Brachionus angularis*.

The Mississippi from Rock Island to Cairo may be divided into two sections as distinguished by plankton production. The upper section, from Rock Island to the mouth of the Missouri, carried a plankton much richer both in species and in numbers than the lower section, between the mouth of the Missouri and the mouth of the Ohio. This is at least in part due to the increase in silt from the waters of the Missouri—an

increase which was distinctly noticeable in the collections. The plankton of the lower section was very similar to that of the Ohio, containing the same predominants, or prevalents, with the addition of *Daphnia longispina*, *Cyclops bicuspidatus*, *Pedalia mira*, and *Brachionus budapestinensis*. The upper section not only contained the same species in greater abundance but, as may be noted in Table 1, contained many other species which are common river predominants.

The Illinois River approaches the physiographic conditions of a mature stream more closely than the Mississippi or the Ohio. According to Kofoed (1903), the Illinois River occupies an ancient and well-worn preglacial channel which causes the stream to have little fall and a slow current. The erosion and turbidity seem to be less than in the Mississippi. Kofoed reports a fall of only 0.13 feet per mile in the Illinois River from Utica, Illinois, to the mouth; while Galtsoff reports a fall of 0.44 feet per mile in the Mississippi from St. Paul to Alexandria. The writer has examined many collections from the Illinois between Utica and the mouth which agree in species and relative abundance with the extensive data collected by Kofoed. In addition to the recent collections made by Mr. R. E. Richardson and the writer, the collections and unpublished data of Kofoed for the years 1896 and 1897 have been recounted and checked by the writer, and tabulated monthly (Table 2). These data, together with those for 1898 published by Kofoed (1908), represent the seasonal distribution of the plankton for perhaps the most mature stream yet studied in North America. Certain species such as *Lysigonium granulatum*, *Polyarthra trigla*, *Keratella cochlearis*, *Diffugia lobostoma*, and *Codonella cratera* are shown to be definitely perennial, existing through all seasons of the years studied. Others are seasonals, appearing regularly at definite periods as discussed later. In general, the plankton is very abundant below the points of pollution. The predominants mentioned as occurring in the Ohio occurred in the Illinois as either perennials or seasonals.

An extensive survey of the summer plankton of the Rock River from near the source to the mouth showed an abundance of the same predominants as found in the Illinois. A series of dams throughout its length creates many pools which serve to stabilize the current. Weekly collections were made at 10-15 mile intervals from the Wisconsin line to the mouth of the river. The specific content of the plankton was found to be the same at different points although there was some variation in abundance due to local conditions. The station at Sterling was selected as being very typical of the Rock River, and the predominant, or prevalent, organisms for the months of June, July, and August, 1926, have been averaged (Table 1). *Trachelomonas volvocina*, *Codonella*

cratera, *Polyarthra trigla*, *Pediastrum duplex*, and many other forms appearing as perennials and seasonals in the Illinois River, appeared in the Rock River abundantly.

Collections from the Fox River at Algonquin, Illinois, made by Mr. R. E. Richardson in the summer of 1916, were counted, averaged, and are tabulated in Table 1. The plankton of the Fox River was rather abundant in both numbers and species and contained most of the predominants found in the Illinois in summer, in nearly the same relative abundance.

A tow made from the Wabash River at Mt. Carmel, Illinois, in the spring of 1927 when the river was at flood stage, contained many of the predominants which occurred at the same season in the Illinois. In all the large streams examined which seem to approach stability, the same plankton predominants occurred, though with some irregularity.

The most abundant or conspicuous of the predominant, or prevalent, species of the plankton of a stable, or permanent, river community in the region studied are as follows:

Algae

Microcystis aeruginosa
Lysigonium granulatum
Scenedesmus quadricauda
Asterionella gracillima
Pediastrum duplex
Closterium acerosum

Protozoa

Trachelomonas volvocina
Diffugia globulosa
Diffugia lobostoma
Codonella cratera
Synura uvella
Stentor coeruleus
Phacus longicauda
Eudorina elegans
Euglena acus
Euglena viridis
Euglena oxyuris
Tintinnidium fluviatilis
Ceratium hirundinella

Cladocera

Chydorus sphaericus
Bosmina longirostris

Daphnia longispina
Moina micrura
Leptodora kindtii

Rotatoria

Polyarthra trigla
Brachionus calyciflorus
Brachionus capsuliflorus
Brachionus angularis
Brachionus budapestinensis
*Brachionus havanaensis*¹
Keratella cochlearis
Keratella quadrata
Notholca striata
Filinia longiseta
Conochiloides natans
Pedalia mira
Asplanchna brightwellii
Synchaeta pectinata
Synchaeta stylata

Copepoda

Cyclops viridis
Cyclops bicuspidatus
Diaptomus pallidus
Diaptomus siciloides

These species occurred either as seasonals or as perennials in the plankton of the Illinois River (Table 2). Most of these were abundantly

¹This species has been confused with *Schizocerca diversicornis* by some investigators and erroneously determined as such.

distributed in all the summer collections examined from the Rock River and many were found in the other large streams discussed. The same species have been reported for the Mississippi by Galtsoff (1924) and for the San Joaquin in California by Allen (1920). They show some seasonal fluctuation, especially in the winter, and many that are never entirely absent may be termed "fluctuating predominants." Plankton organisms are comparable to terrestrial insects in their seasonal distribution. In winter some species usually persist in the adult form in small numbers. Other species exist only as eggs, resting cells, or encysted stages. Ecologically, only those which are in an active stage and influencing the community are important at this season.

IMPOUNDED STREAMS

Observations on the plankton of streams after damming have showed that the impounded water becomes biologically matured. In the many pools on the Rock River created by power dams, each duplicating the hydrographic conditions of a mature stream, the same species of plankton organisms were found to occur as elsewhere in the river, but much more abundantly. The diversion of a small part of the water at Rock Falls, into the Illinois-Mississippi Canal, created a body of water with the ideal conditions of a stable stream. All the disturbing features of stream study, such as fluctuations in current and level, were removed. The water flows at a slow uniform speed and constant gradient, without fluctuations of level, emptying partly into the Illinois and partly into the Mississippi. As the water proceeds down the canal, the same plankton organisms as are found in the Rock River become much more abundant, especially the cladocerans and copepods. The bottom fauna, on the other hand, according to Dr. D. H. Thompson, of the Illinois State Natural History Survey, while of the same composition as that of the river, is relatively much less abundant.

In 1922 a dam was built across the Sangamon River at Decatur, creating a lake one-half mile wide and twelve miles long, commonly known as Lake Decatur. The water averages from six to eight feet in depth. Only at the narrow places where bridges have been constructed can any current be detected. Observations on the plankton just above the present lake showed that only a slight plankton developed when the river was low. As a result of damming the stream, stable conditions have been established and an abundant plankton produced. Since September, 1925, collections either weekly or semi-monthly have been made on the pool at Lost Bridge, two miles above the dam and ten miles below the head of the lake. Previous to 1925, collections were made there from June, 1923, until April, 1924, through the assistance of Prof. A. O.

Weese, then of James Millikin University and now of the University of Oklahoma. The temperature of the water ranged practically the same in all the years studied. In January it remained about 1° C. under the ice. Beginning in February it increased gradually and attained an average of about 28° C. in summer. In August the surface temperatures occasionally reached 30° C. The water at this point was from 15 to 20 feet deep, and the bottom temperature was always about one degree lower than the surface temperature. The pH value was rather steady throughout the year and was always well within the limits of life, generally remaining at about 7.6 and occasionally falling to 7.0 in mid-winter. Dissolved oxygen determinations were made as follows:

Date	Cubic centimeters per liter
August 18, 1928.....	3.25
November 20, 1928.....	9.27
February 22, 1929.....	11.26
June 28, 1929.....	4.10

This showed a high content of dissolved oxygen in winter and a lower content in summer, but always an abundant supply to meet the requirements of the plankton organisms. Birge and Juday (1911) found plankton flourishing in water with 0.5 cc. of dissolved oxygen per liter and found many planktons living very well in water with only 0.25 cc.

The plankton is abundant during the warmer months, but rather scanty during the colder months. The predominant, or prevalent, organisms (Tables 4-7) are the same as those found in the stable rivers mentioned. The greater part of the volume of the summer plankton is composed of *Diaptomus siciloides*, *Cyclops viridis*, *Cyclops bicuspidatus*, *Diaphanosoma brachyurum*, *Brachionus calyciflorus*, *Diffugia lobostoma*, and *Codonella cratera*. Other predominants, such as the common rotifers, *Polyarthra trigla* and *Keratella cochlearis*, although conspicuous in all the collections, do not occupy much of the volume.

The lake was one year old when the plankton was first studied. At this period there was an abundance of chlorophyll-bearing flagellates, particularly *Pleodorina illinoisensis*. Each year there was an apparent tendency toward stability (Table 19). Blue-green algae did not appear until the summer of 1926 and reappeared in the summer of 1928. The number of species of planktons increased from year to year. The outstanding perennials, such as *Keratella cochlearis* and *Polyarthra trigla*, have persisted at all times in the collections. Others, such as *Lysigonium granulatum*, *Diffugia lobostoma*, and *Bosmina longirostris*, first appeared as seasonals and then became established as perennials. *Brachionus calyciflorus* and *Microcystis aeruginosa*, which appeared as perennials

in the Illinois River in 1896, 1897, and 1898, have occurred only as summer forms in Lake Decatur. Some species, such as *Asterionella gracilima*, have not yet appeared. From the fact that new species are appearing each year, it seems that the plankton has not yet reached a climax, or state of maturity, and that probably a community similar to that of a mature river is being established.

No species found in the plankton since 1923 has ever completely dropped out. Even *Pleodorina illinoisensis*, which appeared abundantly in 1923, has since occurred in small numbers, although not abundant enough to be called predominant or prevalent. This continuous progression of species is not "succession" in the same sense as this term is applied to the development of terrestrial communities, but, as will be discussed later, this progression is more comparable to invasion and colonization of a barren terrestrial area. All the predominants so far found in the plankton of Lake Decatur have been found as predominants in the Illinois River. In Lake Decatur, the absence or seasonal variation in distribution of some of the Illinois River predominants may possibly be explained by the difference in the stage of stability.

Galtsoff (1924) in his plankton survey of the upper Mississippi found that there was a great increase in the plankton of the river when it entered Lake Pepin and the lake above the Keokuk dam. In each of these places the waters were impounded over large areas, and the species were the same as elsewhere in the river, but much more abundant. Coker (1929) found that the Entomostraca of the plankton of the Mississippi River increased as the water approached the Keokuk dam.

The plankton element of mature streams may be reproduced by impounding the waters of immature streams so that they may age under more stable conditions. The waters are retained and aged under relatively stable conditions of level and reduced current—all of which are conducive to plankton development and are similar to the conditions of a large and stable stream. The impounded water, being relatively free from the disturbing fluctuations of floods, permits studies to be made that reveal seasonal trends comparable to those in a stable stream. The establishment of the plankton community in impounded waters occupies some time. Many of the species predominant in Lake Decatur in 1928 were present the second year after filling and probably were present the first. The number and abundance of species increased gradually each year until the plankton became similar to that of a stable stream.

YOUNG STREAMS

In an attempt to trace the early development of plankton in young stream communities, streams ranging from 20 to 60 feet in width and

averaging from one to three feet in depth were selected. Their current-speeds ranged from two to five miles per hour, because of the relatively great fall, and were subject to sudden fluctuations. Small rapids and pools characterized their course, because of the irregular erosion of the bed. Plankton collections were made at stations from 20 to 40 miles from the source of the stream; consequently, the water was seldom over 48 hours old and generally less than 24 hours old.

During 1928, semi-monthly collections were made from the Sangamon River at Mahomet, 34 miles from its source (Table 3). Water levels at this station were relative to those recorded at Monticello (Table 9). The normal width of the stream was 50 feet, and the depth averaged 2 feet. The temperature ranged from an average of 9 degrees C. in March to 27.5 degrees C. in August. No collections were made in winter when the river was frozen over. The pH was always 7.6. The dissolved oxygen content, which was higher in summer than that of any of the other stations, ran as follows:

Date	Cubic centimeters per liter
August 2, 1928.....	11.20
November 21, 1928.....	9.32
February 20, 1929.....	8.50
June 28, 1929.....	4.85

Few true plankton organisms occurred in any of the collections. Occasionally a few diatoms or protozoans belonging to the bottom community were found in the collections. During the extreme low water in summer when the current was greatly reduced, a green bloom of *Euglena viridis* formed on a few pools and constituted the only evidence of abundant pelagic organisms.

During part of 1927 and all of 1928, collections were made from the Sangamon River at Monticello, 23 miles below the station at Mahomet and 57 miles below the source (Tables 8 and 9). The river at this point, though practically the same in width, was considerably deeper than at Mahomet, averaging 4 feet, but no differences could be found in the rate of flow.

Water levels (Fig. 8) were averaged monthly from readings made by the U. S. Geological Survey from a gage maintained about one mile below the station. In 1927 the river was high in March, April, May, and June, reaching a low stage in August. In 1928 a low stage was reached in May and remained until December except for several small rises. The temperature showed the usual gradual rise from 2° C. in February to about 26° C. in August. The pH seldom varied from 7.6. The dissolved oxygen determinations were as follows:

Date	Cubic centimeters per liter
August 8, 1928.....	3.25
November 20, 1928.....	9.27
February 22, 1929.....	11.26
June 28, 1929.....	4.10

The first evidence of plankton in the course of the Sangamon occurred at this point. Bottom diatoms were most abundant and, together with a few bottom Protozoa, constituted most of the plankton for December, January, and February. In summer, partly because of the seasonal reduction in the current, true planktons appeared in small numbers. At this time, during the low water stages, many stable river perennials occurred as seasonals. The rotifer *Notholca striata* made its usual spring appearance as in the older streams and designated a scanty spring socies. The plankton, however, even in the summer was never abundant and, as the river bore true planktons only part of the year and many of these were stable river perennials, this point in the stream may be considered as representing the stage of stream succession at which plankton production first develops.

Random collections have been made from other small and apparently young streams in Illinois, including Green River near Geneseo, Deer Creek, and Elkhorn Creek in Whiteside County, Pecatonica River at Pecatonica and Harrison, Kishwaukee River near Rockford, Leaf River near Byron, Stevens Creek near Decatur, Salt Fork at Oakwood, and also from many small streams in Wisconsin, Michigan, Colorado, and numerous other states. Few true plankton organisms occurred in any of the collections. Kofoid (1903) found that a small stream, the Spoon River, near its mouth (75-100 ft. wide) contained very little plankton. The plankton was most abundant in the summer season and consisted chiefly of *Trachelomonas* and *Euglena*. In general, small streams with a swift current contain no evidence of a definite plankton community. The development of a bottom community, however, is indicated by the mollusks and insect larvae seen in all the streams mentioned. In the succession of stream communities, the pelagic community does not appear permanently until the stream has reached some degree of stability.

Not all small streams are young or unstable. During the summer months, small sluggish streams often contain an abundant pelagic population which differs, however, from that of the more mature stream. All the streams of this type examined were dredged ditches draining swampy areas. Consequently, there was little fall, and as there was slight current, the water was much older than that of young streams of similar size and length. Vegetation was abundant in all the streams of this type examined. The Cache River in the southern part of Illinois

was studied in 1928-1929. This stream is mainly a dredged channel (30-40 feet wide, 2-4 feet deep) draining extensive cypress swamps. Usually the current is extremely sluggish; in fact, at times it cannot be detected. Seasonal collections from several points on this stream and from tributary ditches showed an abundant plankton composed largely of chlorophyl-bearing flagellates. Collections made in July, 1926, and September, 1927, from a small sluggish stream (10 feet wide, 2 feet deep) near Deer Grove, Illinois, contained numerous chlorophyl-bearing flagellates and desmids. A channel draining a swampy area west of Erie, Illinois, contained the same type of plankton. Virtually, these streams are only slowly moving shallow ponds.

CONSTITUTION OF THE PLANKTON IN LAKES AND PONDS

Lakes and ponds are bodies of water differing from each other chiefly in depth and distinguished from rivers largely by lack of current. In bodies of still water, aquatic life should reach its greatest development, as here conditions of stability are best. Various types of lakes have long been recognized as containing different types of plankton. Forel (1903) divided European lakes into three types on the basis of temperature. Marsh (1903) recognized distinct differences in the plankton of Green Lake and Lake Winnebago, and noted that deep lakes contained plankton different from that in shallow lakes. Whipple (1898) classified lakes according to amount and duration of surface and bottom temperatures. Birge and Juday (1914) classified lakes according to their respective heat budgets. Thienemann (1926) classified lakes on the basis of bottom predominants. This classification is related indirectly to that used by many European investigators who classify lakes as eutrophic, oligotrophic, and dystrophic according to the amount and origin of detritus and oxygen on the bottom. This is largely determined by depth, and the sum of these and other factors determines the predominant or prevalent species.

A study of the plankton of various types of lakes shows a classification of lakes by plankton predominants correlated to a certain extent with the classification by temperature and depth. The shallow lakes so common in central Illinois, and the moderately deep and truly deep glacial lakes farther north, have certain plankton predominants in common but differ in having others which characterize each of the various types of lakes. Without evidence from the swimming organisms and bottom societies, it is impossible to state whether these belong to three distinct

ecological communities related to one climax or whether they represent the communities of two regional climaxes of formational rank in Illinois and farther north. Temperature, largely influenced by depth and to some extent by climatic differences, seems to be the chief factor differentiating the plankton in these types of lakes. The following discussion, however, is not based primarily on physical factors but on the plankton predominants, or prevalents, which are products of the environmental factors and show ecological relations of the various communities.

SHALLOW LAKES AND PERENNIAL PONDS

In the study of plankton in relation to communities, it is necessary to trace its development in the communities which lead from water to land. As previously mentioned, it is possible to consider ponds and certain lakes as detached or abandoned stream areas. As the conditions in an abandoned part of a stream become more stable, the plankton increases; later when there is no longer any connection with the stream and when littoral conditions appear, the plankton declines. When parts of a stream too young to support a pelagic community are abandoned, they will, if of sufficient area and depth, reproduce the plankton element of a stable stream as far as the size will permit. Later when these parts are reduced by gradual filling by deposition and invasion of terrestrial vegetation, the plankton is supplanted by littoral organisms.

Ponds in this respect may be either detached portions of streams or else natural or artificial reproductions of abandoned areas of streams. Artificial ponds so common in our municipal parks are similar in their plankton composition to ponds of similar size cut off from streams or produced by other natural agencies. Two such ponds at Decatur and at Urbana, because of their availability, were selected for study.

The pond at Decatur was created in 1902 by damming a depression in Fairview Park. It covered nearly three acres and ranged from three to five feet in depth. Collections were made weekly most of the time from October, 1925, until December, 1928. The temperature reading showed a gradual range from nearly 2° C. in February to about 28° C. in August. The pH was generally about 7.6 in summer and sometimes as low as 6.6 in winter. The determinations for the dissolved oxygen content were as follows:

<i>Date</i>	<i>Cubic centimeters per liter</i>
August 19, 1928.....	2.51
November 24, 1928.....	8.14
March 3, 1929.....	9.22

No differences were found in bottom and surface conditions.

The pond at Urbana was created by dredging part of the abandoned channel of the West Branch of the Salt Fork in Crystal Lake Park in 1908. This pond is about one-half mile long and 75 feet wide and has an average depth of four feet. Collections were made regularly from October, 1926, until December, 1928 (Table 11). The temperature ranged from 2° C. in February to 27° C. in August. The pH varied from 7.0 in winter to 7.8 in mid-summer. The determinations for dissolved oxygen were as follows:

Date	Cubic centimeters per liter
August 8, 1928.....	2.00
November 20, 1928.....	5.22
February 22, 1929.....	7.25

In both ponds, it was usually impossible to collect during the month of January, as the ponds were used for skating and cutting of the ice was prohibited. The plankton was similar in both ponds except that *Diaptomus pallidus* was present in the Decatur pond but never in the Urbana pond. Minor differences were noted in many other organisms, but most of the abundant species considered as predominants or prevalents were the same in both ponds and were the same as those found in the plankton of stable rivers. Some forms which were perennials in Kofoid's collections from the Illinois did not show the same seasonal distribution in the park ponds. The plankton was very abundant even in winter under the ice. The dissolved salt content as indicated by dissolved chlorides ran much higher than that of the open waters such as Lake Decatur. These ponds from their lack of outlets would be expected to have a higher salt concentration than waters with open circulation.

Collections from similar artificial ponds at Inverness, Mississippi, at Neosha, Wisconsin, and at Mt. Carmel, Illinois, contained the same plankton predominants. An artificial pond near Mineral, Illinois, created in 1908 by excavating for the embankment of the Illinois-Mississippi Canal, was studied in the summers of 1926 and 1927. This pond covered about one-half acre and was not over two feet deep. The same predominants occurred as in the other artificial ponds.

Collections have been made from many natural floodplain lakes of this depth, most of them old stream oxbows, including Reelfoot Lake in Tennessee, Wolf Lake in Union County, Illinois, and numerous sloughs along the Rock River in northern Illinois (Table 15). Most of the same common predominants occurred as in the other ponds and as in the stable streams. This leads one to the conclusion that for a certain length of time after abandonment, areas of sufficient size support a mature stream population. The primary factor, undoubtedly, is the age of the water and freedom from disturbance by fluctuations in current

and level. In most of the areas studied, there was little or no outflow; consequently, the waters were not of recent origin but were old enough to support a much heavier plankton than that of the stream from which they had originated.

Kofoed found that Thompson Lake and several others on the Illinois River acted, in part at least, as supply reservoirs for the river plankton. His list of species shows no great specific difference between the lake plankton and that of the river. The lakes usually produced a more abundant plankton characterized by more abundant Entomostraca than the river, but the predominant or prevalent species were the same.

Large areas are not alone essential for the existence of the plankton of mature communities. Many small lakes of a size similar to the park ponds described above have been found to bear a plankton which differs in the absence of certain predominants, chiefly the rotifers of the genus *Brachionus*. These ponds contain waters of an acid nature and are surrounded by bogs or swamps. They are similar to bodies of water in the south surrounded by cypress swamps and those of the north connected with tamarack bogs. Collections were made from July, 1928, to August, 1929, on Horseshoe Lake in Alexander County, Illinois; in June, July, and August, 1927, on McIntyre Lake near Money, Mississippi (Eddy and Simer, 1928), and Macon Lake, Three Mile Lake, and Lake Dawson near Inverness, Mississippi (Table 15). All these lakes are from 5 to 15 feet deep and cover hundreds of acres. The shores are swampy and are covered with cypress trees and other vegetation which often extends 100 feet from the land. The pH ranged from 7.0 to 6.4. The plankton contained the same predominants as stable rivers with the exception of the rotifers mentioned. The latter were sometimes present, but in all collections examined they were very scarce. Harring and Myers (1928) report these rotifers as reacting unfavorably towards acidity.

The writer has not had much opportunity to examine the plankton of tamarack bog lakes, his only collections being single collections from Lake County, Illinois, Waukeshaw County, Wisconsin, and San Juan County, Washington. The water of all these lakes was more acid than could be determined on the brom-thymol blue pH indicator set carried by the writer. The water had a characteristic brown color. A "false bottom" of partially decayed organic matter was present in each lake. The plankton was fairly abundant and contained the usual prevalents with the exception of the rotifers of the genus *Brachionus*.

The plankton predominants cited in this paper for shallow lakes and stable rivers are largely based on studies carried on in Illinois and southern Wisconsin. Differences in predominants of such waters due to differing climates are very likely to be found in other latitudes. The

prevalent rotifers of the genus *Brachionus* which are so conspicuous in the Illinois and Rock River and in shallow lakes of the same vicinity are scarce or lacking in the writer's observations on southern waters (Eddy, 1931). Recent observations in central and northern Minnesota show them to be very rare in shallow lakes and large streams. If species of *Brachionus* are associational predominants, or prevalents, this seems to indicate a difference in predominants from north to south and suggests a change in the association.

TEMPORARY PONDS

The successional trend of such lakes and ponds as have been previously discussed is to fill gradually until they become too shallow to hold enough water to last through periods of drought. They then become temporary ponds, containing water only during the wet seasons of the year. Vegetation, particularly button bush and willow, often invades the ponds studied at this stage.

Murray (1911) made a study of the annual distribution of the organisms of a temporary, or periodic, pond near Glasgow. The plankton and bottom fauna were mixed to such an extent that it was impossible to distinguish between them. The predominant or prevalent species were in many cases either the same as, or closely related to, those found in the ponds studied by the present writer. Prevalents appeared in the Glasgow pond almost as soon as the pond filled but did not become abundant until the water was warm.

An oxbow pond north of Urbana, Illinois, was studied in 1927 and 1928 (Table 12). This pond was one of a series left in the old channel of the West Branch of the Salt Fork by the construction of a drainage ditch in 1908. Smartweed and willow were abundant in it. When full of water it was about a foot deep and 15 feet wide by several hundred feet long. Each year it filled in October and dried up in August. During the winter months it was frozen to the bottom and no pelagic life of any kind could be found. The temperature when the pond thawed in January or February ranged from 0.5° to 3° C. and gradually increased, reaching 28° C. in August. The summer pH was around 7.6, and the winter pH was 7.4-7.1. No tests of dissolved oxygen were made, but from the amount of submerged vegetation it is very probable that this was high, at least in the warmer months.

Series of collections were made on three temporary ponds on the prairie west of Seymour, Illinois, during the wet season of 1926, through the assistance of Dr. Martha Shackelford. Also in 1928, collections were made in the largest of these ponds in the wet season (Table 13). The temperature ranged from freezing in winter to 28° C. in summer. The

shallow ponds such as this and the preceding showed more daily fluctuation in temperature than was noticed in the deeper bodies of water studied. The pH usually remained about 7.6. Only one dissolved oxygen determination was made, on November 26, 1928, when the ice was one inch thick. The reading was only 1.55 cc. per l. At that time the pond had been filled only four weeks and the vegetation had not resumed its growth. The dissolved oxygen content probably would run higher in warmer months because of the large amount of submerged vegetation.

Seasonal conditions similar to those in the Urbana pond existed here when the ponds filled in the fall. Bottom and pelagic organisms soon appeared and formed communities (Fig. 7), which later disappeared when the ponds froze solid. In late February or early March these communities again appeared with the thawing of the ice and persisted until the complete drying up in August.

All these temporary ponds contained a questionable plankton insofar as there were only a few species of true pelagic organisms. Bottom or vegetation forms were common and abundant. This aggregation of organisms should be considered, however, as they are comparable to plankton and represent the last trace of plankton before it entirely disappears as the aquatic community merges into the terrestrial community. All the different ponds agree in the presence of certain predominants. The cladoceran *Camptocercus rectirostris* and the copepod *Cyclops serrulatus* and several undetermined species of *Canthocamptus* are characteristic of ponds of this type only. Other prevalents which occasionally occur also in other bodies of water are various species of *Simocephalus* and *Ceriodaphnia*. *Chydorus sphaericus*, *Cyclops bicuspidatus*, *Trachelomonas volvocina*, *Notholca striata*, *Scenedesmus quadricauda*, *Synura uvella*, are forms which are prevalent both in temporary ponds and in mature streams. Rotifers are seldom abundant and generally consist of bottom species, especially those of the genus *Monostyla*. The protozoans are usually bottom forms, although chlorophyll-bearing flagellates are very abundant in summer. The same predominants were found in random collections made from temporary ponds elsewhere in Illinois, namely, at Cerro Gordo, Muncie, Erie, and Amboy.

The bottom fauna is abundant in these ponds, but with the loss of depth the pelagic society has largely disappeared. Kofoed found that, in general, waters rich in submerged macro-flora produced less plankton than those free from vegetation. Mere size has little to do with plankton production except where littoral influences creep in as the area contracts. Collections in cross-section from Lake Decatur showed no marked differences until entering the littoral areas at the shores. In this area

where the aquatic habitat merged into land, the plankton contained the same predominants as found in temporary ponds. The pelagic socies appears after the bottom socies in the developing community of a young stream and disappears before the bottom socies in the terrestrial succession of an abandoned portion of the stream. When a stream is turned into a new channel, as in the Illinois-Mississippi Canal, or when a young stream is prematurely aged, as at Decatur, the pelagic socies develops before the bottom. This is probably because the pelagic conditions essential for maturity are prepared sooner than those of the bottom.

A striking instance of the persistence of plankton in a shallow pond was found near Monticello in the summer of 1928. A few random collections were made there from a pond which was about 40 feet in diameter and 6 inches in depth, and which had a deep-mud bottom and no vegetation. Although this pond was well on its way towards becoming land, the plankton was very similar to that of larger and more permanent ponds or stable streams.

In a series of southern Illinois sink-hole ponds demonstrating succession from pond to land, the last stage, where the pond contained only 6 inches of water during the wet seasons, supported a few plankton organisms mingled with bottom forms (Eddy, 1931). A pond a foot deep showing an earlier stage, also filled only in wet seasons, retained plankton similar to that of the perennial ponds. Apparently some planktons are very tenacious of their habitats, appearing as long as there is water to live in.

Shallow permanent ponds, located where the water table is high enough to keep them filled through the dry season, may have the same types of organisms as temporary ponds. Several such ponds, to be discussed later under succession of large lakes, were studied near Gary, Indiana. These ponds, although containing water all the year, have the same predominants as the ponds which exist only in the wet seasons. The cypress swamps in the southern part of Illinois have been studied by the writer and have been found to contain a plankton somewhat different from that of temporary ponds. The water is shallow throughout the year and filled with vegetation, but many true plankton organisms occur. Many of the prevalents are the same as those of stable streams, with the exception of the rotifers of the genus *Brachionus*. Chlorophyl-bearing flagellates are particularly abundant most of the year in these swamps. The rotifer *Trochosphaera aequatorialis*, which was seldom found in collections from other waters studied, is often abundant there in the summer plankton.

DEEP GLACIAL LAKES

Although this study of plankton is based chiefly on data from the region of Illinois and the lists of community predominants apply to the waters of this region, it is of interest to consider data from other bodies of water which have, at least in part, ecological conditions similar to those of Illinois.

Numerous lakes of glacial origin, many of them very deep, are found in the northern states and Canada. Some occupy depressions in the ground moraine; others occupy depressions caused by melting of buried masses of ice left by receding ice sheets. Some occupy valleys between terminal moraines; others preglacial valleys which have been dammed by glacial deposits. Many of these lakes have outlets and tributaries.

The depth of glacial lakes varies from a few feet to several hundred feet. Many of the shallow lakes show that they were formerly quite deep and have been filled by deposition and by lowering of the water table. Extremely deep lakes, in which the temperature of the water below the thermocline shows little seasonal fluctuation, are the youngest type ecologically. As this type of lake gradually fills, the volume of the hypolimnion is reduced sufficiently for the temperature to fluctuate with the seasonal changes in the epilimnion, and it gradually changes to the shallower and warmer type of lake. Many of our moderately deep lakes undoubtedly were once very deep lakes. Juday (1914) describes many of these lakes as being extinct, having passed into marshy meadows of peat underlaid with marl.

Glacial lakes are often classified according to types of bottom (rock, clay, sand, etc.). The chemical and physical composition of the water resulting from the type of bottom or drainage area usually alters the type of plankton. The writer is inclined to believe that further study of the plankton of glacial lakes with various types of bottom and drainage basins will show that the resulting plankton communities represent stages of different seres and belong to the same regional climax. No data are presented in this paper in regard to types of bottoms and their relations to plankton communities. The glacial lakes studied by the writer were usually in sand and clay drift.

The plankton of these lakes may be divided according to predominants into two classes: that of very deep lakes, and that of shallow or moderately deep lakes. This grouping corresponds roughly with Whipple's classifications (Whipple, 1898). The deep lakes are those of the first order, and the moderately deep and shallow lakes belong to the second and third orders.

The ecological status of these lakes based on succession is very difficult to ascertain, although a study of their plankton shows that they have many characteristic organisms. Physiographically, they are not permanent, as dead or dying lakes are common throughout our northern and western states. The largest and deepest of these lakes, such as the Great Lakes, apparently are permanent, but even here we find evidence that the water has lowered and that portions of the lake have been converted into land. This process is not to be compared to the abandoning of an area by a river which, being motile, simply moves over into another area where the communities of the particular stream continue to exist.

A physiographic analysis of such lakes shows that, as they often have one or more streams entering at one end and leaving at the other, they may be considered as enlarged portions of streams (Marsh, 1903). Enlarged portions of certain large streams, such as Lake Keokuk or Lake Pepin, do not contain the same type of plankton as do these deeper glacial lakes, but retain the type of plankton found in the river. This difference may be due to depth, which in turn causes a lower and more uniform temperature in the deeper lakes.

If a stream can be matured by holding back the water as previously demonstrated, then each small stream when enlarged into a deep glacial lake should develop a replica of a mature or permanent stream community. But the tendency of any body of impounded water is to fill and to end eventually as the original stream, so that such a body is not permanent but only duplicates temporarily the conditions of a stable stream. Although very little has been done on the far northern streams of North America to determine their plankton composition, the few samples seen by the writer make it seem improbable that they bear plankton similar in specific composition to that of our deep glacial lakes.

A few random collections from the Mississippi River above Minneapolis, however, indicate that the predominant species are not the same as those in the river farther south, but are more like those of northern glacial lakes. Diatoms are conspicuous. Rotifers are scarce, Synchaeta, Polyarthra, and Keratella being the prevalent forms. No species of Brachionus were found.

The relation of the plankton of glacial lakes to the plankton of the stable river of the same region is uncertain, largely because of lack of information regarding northern stream plankton. It is entirely possible that the plankton of these lakes bears the same relation to the plankton of the stable river as exists between the plankton communities of lakes and rivers studied farther south. Although the plankton of these lakes is essentially different from that of all streams we know, their communi-

ties still may be considered as developmental stages in stream succession. By an alternative interpretation they are edaphic mature communities, especially the Great Lakes, whose permanence will depend on local conditions. In either case they should be accorded the rank of associes.

The plankton organisms of some of these lakes, for example, Lake Michigan, Lake Erie, Finger Lakes, Green Lake, Lake Mendota, and Lake Winnebago, have been described by Ward (1896), Marsh (1903), Birge and Juday (1914, 1921, 1922), Eddy (1927), and Fish (1929). The writer has examined many random collections from glacial lakes including collections from Lake Superior at Duluth, Minnesota, Lake Winnebago and Oconomowoc Lake in Wisconsin, Douglas Lake in Michigan, Sand Lake and Long Lake in Illinois, and many lakes in Minnesota. Most of these lakes are relatively deep, and many have a thermocline in summer. The plankton is definitely characterized by the presence of certain predominant species (Table 16) which seldom or never occur in rivers. Many but not all of the river predominants, previously described, occur in these lakes, showing an ecological relationship. The following species are common fluctuating predominants in the glacial lakes, showing some variation in abundance in the different seasons. Those with an asterisk are characteristic of the deeper lakes only.

Protozoa

Diffugia globulosa
Ceratium hirundinella
Codonella cratera
Dinobryon sertularia

Algae

Lysigonium granulatum
Asterionella gracillima
*Striatella fenestrata**
Fragilaria crotonensis
Scenedesmus quadricauda
Pediastrum duplex

Cladocera

*Bosmina longispina**
*Daphnia retrocurva**
Daphnia longispina
var. *hyalina**
Chydorus sphaericus

Rotifera

Polyarthra trigla
Keratella cochlearis
Keratella quadrata
*Notholca longispina**
Notholca striata
Asplanchna priodonta
Synchaeta stylata

Copepoda

*Diaptomus ashlandi**
*Diaptomus sicilis**
Diaptomus oregonensis
*Diaptomus minutus**
*Epischura lacustris**
Cyclops viridis
Cyclops bicuspidatus
*Cyclops leuckarti**
*Limnocalanus macrurus**

The predominants listed above show considerable variation in their distribution, not all occurring in each lake but occurring with sufficient regularity in a large proportion of the lakes examined to definitely establish their prevalence. In spite of considerable fluctuation of predominants, it is easy to distinguish two definite groups of plankton by

their predominants. Plankton containing *Striatella fencstrata*, *Notholca longispina*, *Diaptomus minutus*, and others marked with an asterisk, in addition to other predominants found in rivers and lakes alike, is usually that of a lake with a depth sufficient to keep the temperature of the water relatively low. Moderately shallow glacial lakes even with a thermocline usually do not have these deep lake prevalents, at least not in abundance, but bear a plankton which is similar to the river type, differing, however, from the river and shallow lake type previously described from Illinois by being rich in diatoms and poor in rotifers, especially *Filinia longiseta* and species of *Brachionus*. *Codonella cratera*, so common in rivers, is never abundant in these lakes.

The difference between these two types of glacial lakes can easily be seen by comparing the plankton of Lake Michigan and Lake Superior with that of moderately deep glacial lakes (Table 16). The plankton of Lake Michigan and Lake Superior shows some difference from the shallower glacial lakes in the predominant species of copepods, one of which, *Cyclops leuckarti*, appeared much more abundantly in the smaller lakes and in Lake Erie (Fish, 1929) but has not been reported for the other Great Lakes. In the collections examined, *Epischura lacustris* and *Diaptomus minutus* occurred more abundantly in the Great Lakes and other deep lakes.

Diaptomus sicilis and *Diaptomus ashlandi* have been reported from deep lakes only. *Diaptomus oregonensis* occurred only in the shallow glacial lakes and seemed to replace *Diaptomus pallidus* and *Diaptomus siciloides*, which are predominants in shallow lakes farther south. The rotifers *Notholca striata* and *Keratella quadrata* were present more or less sporadically throughout the year, although they occur as vernal predominants in the more shallow southern lakes.

Marsh (1903) compared the plankton of Green Lake in Wisconsin with the plankton of Lake Winnebago. Green Lake is about 7 miles long and 2½ miles wide, with a mean depth of 33.1 meters and a maximum depth of 72.2 meters, or 237 feet (Juday, 1914). Lake Winnebago is about 10 miles wide and about 28 miles long but has an average depth of only 4.7 meters with a maximum of 6.4 meters, or 21 feet. Marsh found that the plankton of Green Lake was characterized by certain organisms such as *Diaptomus sicilis*, *Diaptomus minutus*, and *Limnocalanus macrurus*, while *Mysis* and *Pontoporeia* were found in the abyssal portions. The plankton of Lake Winnebago was characterized by *Diaptomus oregonensis*, *Conochilus volvox*, and the stable river predominants *Codonella cratera*, *Daphnia pulex*, and *Daphnia longispina* var. *hyalina*. Many forms were common to the plankton of both lakes but

were more abundant in the deeper lake, for example, *Ceratium hirundinella*, *Notholca longispina*, *Leptodora kindtii* and *Diaphanosoma brachyurum*. This indicated that these organisms are more prevalent in deep lakes. On the other hand, many forms which are commonly found in river plankton, such as *Asplanchna*, *Polyarthra*, *Synchaeta pectinata*, and *Chydorus*, Marsh found to be more abundant in Lake Winnebago. He found also that they had a much longer season of abundance than in the deeper lakes.

In a similar way, Nordquist (1921) found it possible to distinguish the plankton of various types of Swedish waters by the predominants. He found the plankton of ponds or shallow lakes characterized by *Brachionus pala* (*B. calyciflorus*), *Brachionus urceolaris* (*B. capsuliflorus*), *Brachionus angularis*, *Schizocerca diversicornis*, *Pedalia mira*, *Daphnia pulex*, *Daphnia longispina*, *Ceriodaphnia pulchella*, and *Diaptomus vulgaris*. Most of these are the same species as found by the writer to be predominant in the shallow lakes and rivers discussed in this paper. Nordquist found lakes (deeper than ponds) to be characterized by *Notholca longispina*, *Daphnia longispina* var. *hyalina* and var. *cucullata*, *Bosmina coregoni*, *Leptodora kindtii*, *Cyclops oithonoides*, and *Diaptomus graciloides*. These predominants apparently determine the plankton of glacial lakes with no distinction as to deep or moderately deep glacial lakes. Many species, such as *Conochilus volvox*, *Asplanchna priodonta*, *Asplanchna brightwellii*, *Synchaeta pectinata*, *Polyarthra platyptera*, *Triarthra longiseta*, *Anuraea cochlearis*, *Anuraea aculeata*, *Diaphanosoma brachyurum*, *Bosmina longirostris*, *Cyclops strenuus*, *Cyclops leuckarti*, and *Diaptomus gracilis*, were found to be common to both ponds and lakes.

The plankton fauna reported by Kemmerer, Bovard, and Boorman (1923) for the deeper lakes of Washington, Oregon, California, and Idaho, contains predominants similar to those present in the northern glacial lakes. The following species appear often in the collections made by these investigators, and many probably bear the status of perennials, although the observations were limited to summer collections only.

Rotifera

Notholca longispina
Polyarthra trigla
Anuraea cochlearis
Anuraea aculeata

Copepoda

Epischura nevadensis
Cyclops bicuspidatus
Cyclops viridis
Diaptomus oregonensis

Cladocera

Daphnia longispina
Diaphanosoma leuchtenbergianum

These predominants are either the same species as, or closely related to, those found in the northern glacial lakes. The rotifer *Keratella* (*Anuraea*) *aculeata* is abundant in the spring plankton of Lake Michigan, and Kofoed also reports it as a spring form in the Illinois River. The copepod *Epischura nevadensis* replaces *Epischura lacustris* entirely in the western states. The cladoceran *Diaphanosoma leuchtenbergianum* is a questionable species and is probably the same as *Diaphanosoma brachyurum*, which occurs abundantly in the plankton of northern and eastern glacial lakes.

Collections made by Professor Frank Smith from mountain lakes in the vicinity of Tolland, Colorado, and by Professor S. A. Forbes from Yellowstone Park, were examined by the writer and found to contain in general the same type of plankton organisms as did the collections from the northern glacial lakes. The predominants from the collections from lakes in Colorado and Yellowstone Park are as follows:

<i>Cyclops leuckarti</i>	<i>Diaptomus oregonensis</i>
<i>Cyclops viridis</i>	<i>Epischura nevadensis</i>
<i>Cyclops bicuspidatus</i>	<i>Diaphanosoma brachyurum</i>
<i>Keratella cochlearis</i>	<i>Daphnia longispina</i>
<i>Polyarthra trigla</i>	<i>Daphnia retrocurva</i>
<i>Diaptomus leptopus</i>	<i>Asterionella gracillima</i>
<i>Diaptomus shoshone</i>	<i>Ceratum hirundinella</i>
<i>Diaptomus ashlandi</i>	

The factor of temperature has been mentioned as partly responsible for the differences in the fauna of these lakes from that of more shallow lakes or rivers in the same vicinity. Shallow lakes from which collections were made in the vicinity of Oconomowoc Lake in southern Wisconsin contained stable-river predominants, while the deeper Oconomowoc Lake itself contained both stable-river and deep-lake predominants (Table 20). Deep lakes form perhaps the most stable habitat of all fresh-water bodies. Forbes (1883) found that the conditions of life in Lake Michigan were remarkably uniform throughout the seasons and from year to year and that both plant and animal life exhibited there a regularity and stability in remarkable contrast to their fluctuations in smaller bodies of water and on land.

Shelford (Ward and Whipple, 1918) has pointed out that Lake Michigan, being a large and deep lake, has none of the seasonal temperature changes extending to the deeper parts. Consequently, as only the surface temperature fluctuates, one would expect the deeper portions to exert a greater stabilizing influence on the surrounding waters than would be found in the waters of more shallow lakes. The greatest factor, besides depth, differentiating these lakes from the shallow lakes is that of temperature. The deep lakes of Africa (West, 1907) with a high

temperature do not contain the same types of plankton organisms as found in our deep glacial lakes, but have a plankton more similar in content to that of our large rivers and shallow lakes. West mentions that this is indicative of the importance of temperature. Depth, however, is the primary factor, controlling temperature, which is a secondary factor.

Abandoned areas of glacial lakes and entire deep glacial lakes often show various stages of succession to land. A series of ponds on ridges of different ages were studied at the south end of Lake Michigan on the old Calumet beach near Gary, Indiana. In early post-glacial times, Lake Michigan occupied a much larger bed; and as the lake receded it left many beaches, the remains of which now appear as a series of sand ridges paralleling the present contour of the lake. The ponds selected for study were beyond ridges 1, 5, 14, 60, 93, 94, 95, and 96, numbered successively from the lake. These ponds are narrow, 10 to 20 feet wide, shallow and very long, extending out of sight between the ridges. Ponds 1 and 5 are comparatively free from vegetation and are about two feet deep. The other ponds range from six to twelve inches in depth and are filled with vegetation, chiefly buttonbush. The water level remains the same in the ponds throughout the year, but their general appearance is that of temporary ponds.

Collections were made in May of three years, 1927, 1928, and 1929 (Table 14). *Arcella vulgaris*, *Monostyla lunaris*, *Daphnia pulex*, *Cyclops serrulatus*, and species of *Simocephalus* and *Canthocamptus*, all of which are predominants characteristic of temporary ponds, were common in all the collections. Predominants such as *Chydorus sphaericus*, *Cyclops viridis*, and *Cyclops bicuspidatus*, which are prevalent in both temporary ponds and stable rivers, were abundant. Pond 1, nearest the lake, was polluted to some extent by a cement plant, so that the plankton may have been altered. Otherwise, the ponds nearest the lake showed evidence of their origin in the presence of a number of species which are predominant or abundant in Lake Michigan. *Ceratium hirundinella*, *Diaphanosoma brachyurum*, *Bosmina longirostris*, *Fragilaria crotonensis*, *Polyarthra trigla*, and *Keratella cochlearis* occurred in ponds 5 and 14. All these are species which are predominant in Lake Michigan and in stable rivers but not in temporary ponds. None of the species occurred which are predominant in deep lakes only and which characterize the plankton of Lake Michigan. Possibly they were unable to survive the change.

A single series of collections was made in September, 1927, from three lakes in Waukesha County, Wisconsin, (Table 20) which showed three stages of succession towards land. Although the data were scanty, they indicated the general trend of succession. The deepest and youngest was Oconomowoc Lake, which is a typical moderately deep lake

having a mean depth of 9.5 meters and a maximum depth of 19.1 meters, or 62.6 feet (Juday, 1914; Smith, 1920). Pewaukee Lake has an average depth of 3.9 meters with a maximum of 13.8 meters, or 45.3 feet. Lulu Lake, situated in the center of a large bog, represents the remains of a lake which, from the evidence of the old shore lines, formerly covered many miles and had a depth of over 80 feet. Lulu Lake is about 6 feet deep and has a soft bottom, the depth of which was not determined. This lake was acid, while the others were slightly alkaline with a pH of 7.6. The predominants of the plankton of Oconomowoc Lake were the same as for other moderately deep glacial lakes. Those of Pewaukee and Lulu lakes were more like those of stable rivers or the shallow lakes of Illinois, with the exception of the rotifers of the genus *Brachionus*, which did not appear in the collections. From the stage represented by Lulu Lake, the next stage of succession would be a very shallow bog pond. The data on this type of plankton, though scanty,¹ suggest that it has a succession similar to that of plankton in the abandoned channel of a stable river. Apparently, the general trend of succession of plankton in deep lakes is to that of shallow lakes and then to that of temporary ponds. *Keratella cochlearis*, *Polyarthra trigla*, and *Pediastrum duplex* occur as perennial predominants in the deep lakes but are not as abundant as in stable rivers. The presence of these prevalents in both types of waters indicates that these lakes occupy the status of developmental associates. The predominants characteristic of the deep glacial lakes serve to distinguish this associates from the river communities. As demonstrated by the developmental series in Oconomowoc and Lulu lakes, parts of deep lakes are similar to the ponds or abandoned areas of streams, as they also approach a terrestrial climax.

SEASONAL COMMUNITIES AS INDICATED BY PLANKTON ORGANISMS

In all the bodies of water studied throughout the seasons of the year, seasonal communities could be distinguished in the plankton by the presence of abundant organisms which may be termed "seasonals." Such communities, if mature, are usually called "societies," and if existing within an immature community they are called "societies." Seasonals should appear at certain periods and become conspicuous through their abundance or size, thus indicating the presence of a definite group of

¹Since this work was prepared for publication, the writer has collected a large quantity of data on glacial lakes of various depths which show the same successional trend. In many cases the pond type of plankton was not reached until the lake had become very shallow.

organisms influenced, in part at least, by particular seasonal factors. Seasonals are doubtless of considerable importance, and in view of their numbers or size they must exercise some influence on other members of the community. During their absence or period of inactivity they probably exist as eggs, spores, or encysted forms.

STABLE STREAMS AND PERENNIAL PONDS

Seasonal socies in streams are best studied under the controlled conditions produced by dams, inasmuch as the periodic floods under natural conditions may destroy or disturb the pelagic community before the plankton seasonal element has had time to develop. Even in the lake at Decatur, where the water level never fluctuated more than three feet, floods in the stream above increased the current so that the age of the water was at times reduced to that of water supporting very little plankton.

In large streams such as the Illinois River, where floods dilute the plankton but where much of the water is quite old because it has traveled from distant tributaries, seasonals still can be distinguished, although their abundance may be reduced. It was found that seasonal societies could be easily studied in undisturbed areas, such as lakes, artificial ponds, canals, or abandoned areas of streams, especially if such bodies were not subject to fluctuations of level. Such results were then compared and checked with those of a normal stream.

An attempt is made in Figs. 1-7 to represent graphically the relative volume of the seasonal, perennial, and incidental organisms composing the plankton in various types of waters for one or more years. Because of the great variations in volume, it was necessary to use a modification of the method of Lohmann as described by Birge and Juday (1922). The height of each curve represents the radius of a sphere whose volume is equal to the volume of the group of organisms. The radius may be determined by the formula, $R = \sqrt[3]{\frac{v}{4.19}}$, where v is the volume of the sphere, or in this case, the number of cubic millimeters of plankton. In order to secure graphs of convenient dimensions, it was necessary to employ a scale representing .01 cubic millimeter of plankton by a radius of .25 centimeter in Fig. 1 and .25 millimeter in Figs. 2-7. All these figures have been reduced to one-fourth the original scale for reproduction here.

Four seasonal societies or socies were found in all of the stream and pond communities studied throughout the year. The seasonal socies did not recur at the same dates in successive years, but sometimes varied as much as a month. Overlapping was a common feature, organisms

from the preceding species persisting in small numbers for several months after their maximum abundance was past.

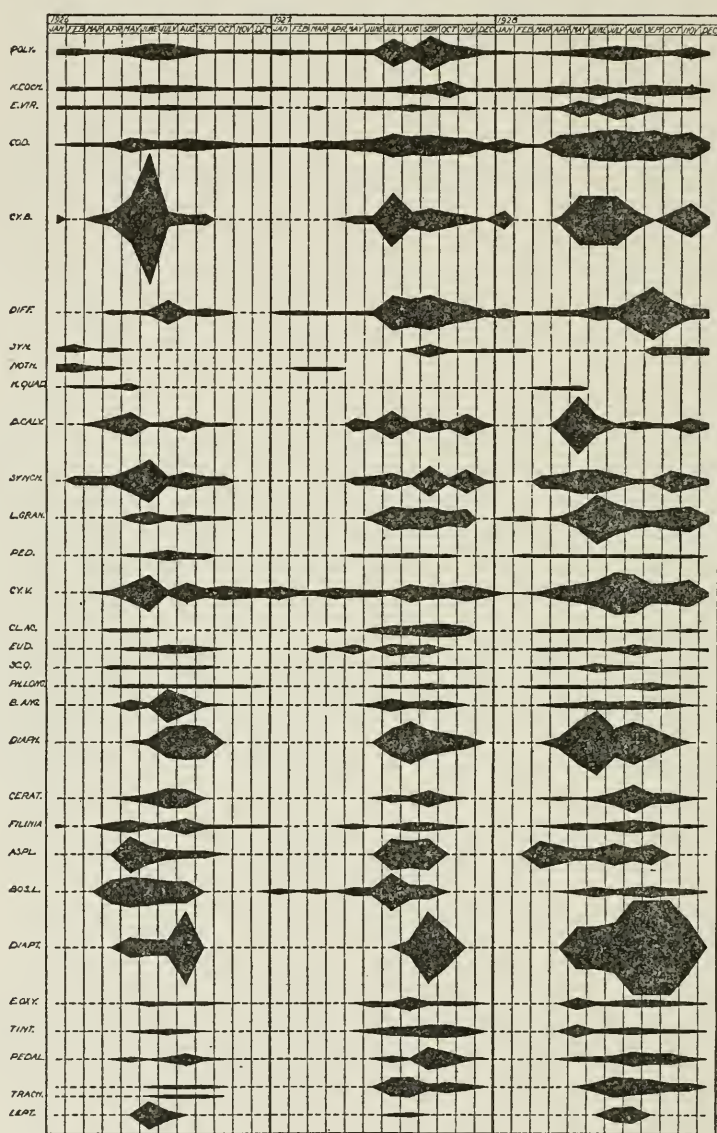


FIGURE 1

Graphs showing relative volume of predominant organisms in the plankton of Lake Decatur, 1926, 1927, 1928. (For graphical method, scale, and reduction, see text, page 37.) A key to the symbols at the left is supplied on the opposite page.

The hiemal socies usually started the last part of December and continued until April, when the vernal socies was well established. The plankton organisms of the hiemal socies were general scanty. Diatoms were common. Minute flagellates and a few ciliates, such as *Stentor*, were conspicuous. Perennials such as *Polyarthra trigla*, *Keratella cochlearis*, and *Codonella cratera* were scarce. *Synura uvella* was characteristic, often appearing late in January and remaining until April or May. Occasionally *Notholca striata* and *Cyclops bicuspidatus*, which properly belonged to the vernal socies, appeared in January, but they were never abundant or conspicuous until later in the spring. The plankton seasonals probably appear much earlier in the south than in the north, although no evidence has been published on this point. From data collected by the writer for the Illinois State Natural History Survey from Horseshoe Lake near Cairo, Illinois, 250 miles south of most of the areas reported in this paper, there is very little evidence of a hiemal socies. Hiemal forms such as *Stentor* spp. and *Synura uvella* are present during the month of January only, and the vernal socies has begun to be established by the first of February. Temperature is undoubtedly the most important factor limiting the hiemal socies. The temperature of all the waters studied in winter remained at 0.5° C. when covered with ice during January and February. Tests made through the ice always showed that there was sufficient dissolved oxygen to support plankton. The turbidity was usually low, and the pH value never fell more than slightly in winter. Light is well recognized as one important factor which is limited in winter, not only by the shorter days but also by the greater angle of incidence.

With the increase in temperature in the latter part of February, the perennials increased in abundance, and in March the seasonals of the vernal socies usually appeared. In the park ponds at Decatur and Urbana, the vernal community was well established by the end of February.

KEY TO SYMBOLS USED IN FIG. 1

POLY.....	<i>Polyarthra trigla</i> Ehr.	SC. Q.....	<i>Scenedesmus quadricauda</i> (Turp.) Bréb.
K. COCH.....	<i>Keratella cochlearis</i> (Gosse)	PH. LONG.....	<i>Phacus longicauda</i> (Ehr.) Duj.
COD.....	<i>Codonella cratera</i> (Leidy) Vorce	B. ANG.....	<i>Brachionus angularis</i> Gosse
CV. B.....	<i>Cyclops bicuspidatus</i> Claus	DIAPH.....	<i>Diaphanosoma brachyurum</i> (Liéven)
DIFF.....	<i>Diffugia lobostoma</i> Leidy	CERAT.....	<i>Ceratium hirundinella</i> O.F.M.
SYN.....	<i>Synura uvella</i> Ehr.	FILINIA.....	<i>Filinia longiseta</i> (Ehr.)
NOTH.....	<i>Notholca striata</i> (O.F.M.)	ASPL.....	<i>Asplanchna</i> spp.
K. QUAD.....	<i>Keratella quadrata</i> (O.F.M.)	BOS. L.....	<i>Bosmina longirostris</i> O.F.M.
B. CALY.....	<i>Brachionus calyciflorus</i> Pallas	DIAPT.....	<i>Diaptomus siciloides</i> Lillie.
SYNCH.....	<i>Synchaeta</i> spp.	E. OXY.....	<i>Euglena oxyuris</i> Schmarda
L. GRAN.....	<i>Lysigonium</i> (<i>Melosira</i>) <i>granulatum</i> (Ehr.) Kuntze	TINT.....	<i>Tintinnidium fluviatilis</i> Stein
PED.....	<i>Pediastrum duplex</i> Meyen	PEDAL.....	<i>Pedalia mira</i> (Hudson)
CV. V.....	<i>Cyclops viridis</i> Jurine	TRACH.....	<i>Trachelomonas volvocina</i> Ehr.
CL. AC.....	<i>Closterium acerosum</i> (Schrk.) Ehr.	LEPT.....	<i>Leptodora kindtii</i> (Focke)
EUD.....	<i>Eudorina elegans</i> Ehr.		

The characteristic rotifers *Keratella quadrata* and *Notholca striata* often appeared early and remained until May or June. Many of the hial forms persisted in small numbers through this period. *Cyclops bicus-*



FIGURE 2

Graphs showing relative volume of principal plankton groups in Lake Decatur, 1926, 1927, and 1928. (For graphical method, scale, and reduction, see text, page 37.)

pidatus became the characteristic and abundant copepod. *Daphnia longispina*, *Synchaeta pectinata*, *Conochiloides natans*, *Filinia longiseta*, and *Pediastrum duplex* usually appeared at this time and persisted through the summer.

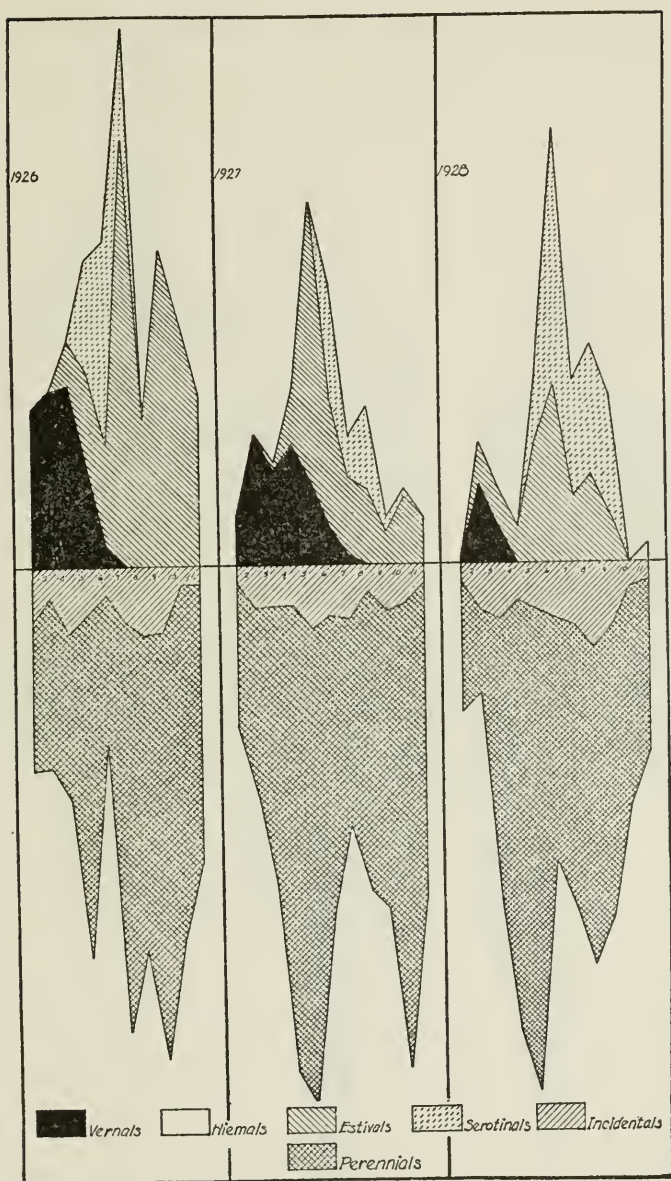


FIGURE 3

Graphs showing relative volume of principal plankton groups in the Park Pond at Decatur, 1926, 1927, and 1928. The blank spaces for January represent periods when the ice prevented collecting. (For graphical method, scale, and reduction, see text, page 37.)

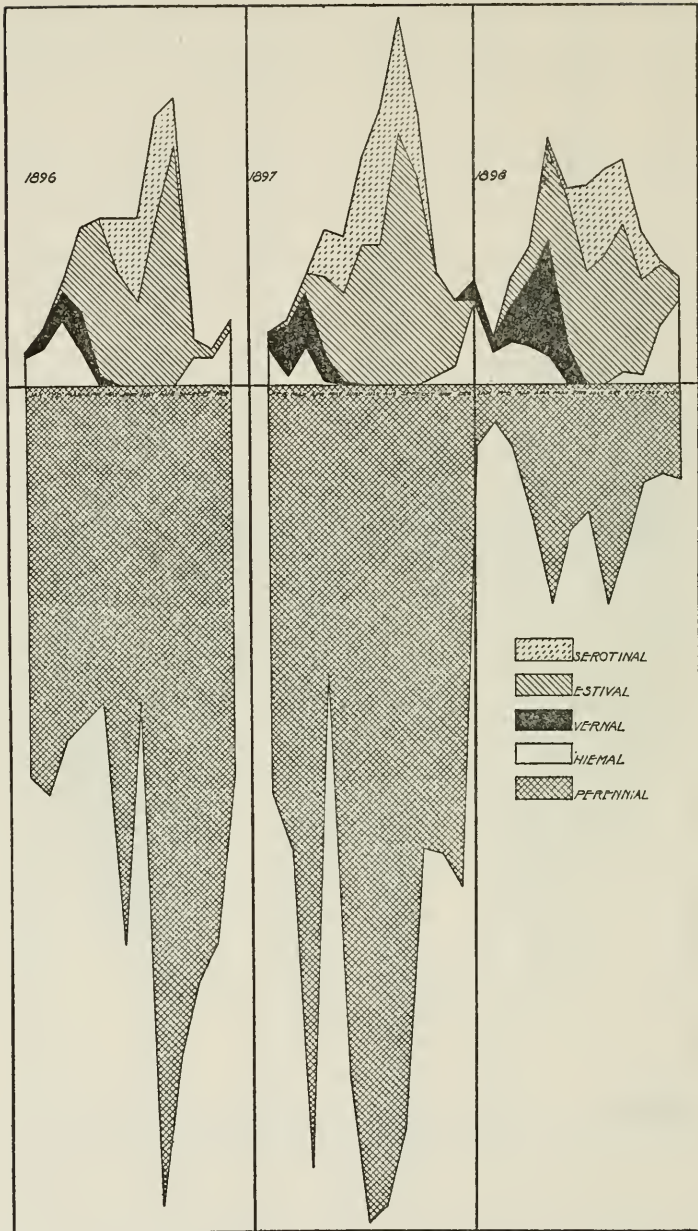


FIGURE 4

Graphs showing relative volume of principal plankton groups in the Illinois River, 1896, 1897, and 1898 (data from Kofoid). The volume of the perennial organisms was so great that it was impossible to add that of the incidental organisms. (For graphical method, scale, and reduction, see text, page 37.)

In May and June other plankton organisms appeared in abundance and formed an indefinite estival socies generally characterized by species of *Brachionus*. *Diaphanosoma brachyurum*, *Diaptomus siciloides*, *Diaptomus pallidus*, and many chlorophyl-bearing flagellates appeared at this time. Many of the forms present then persisted until late in the autumn.

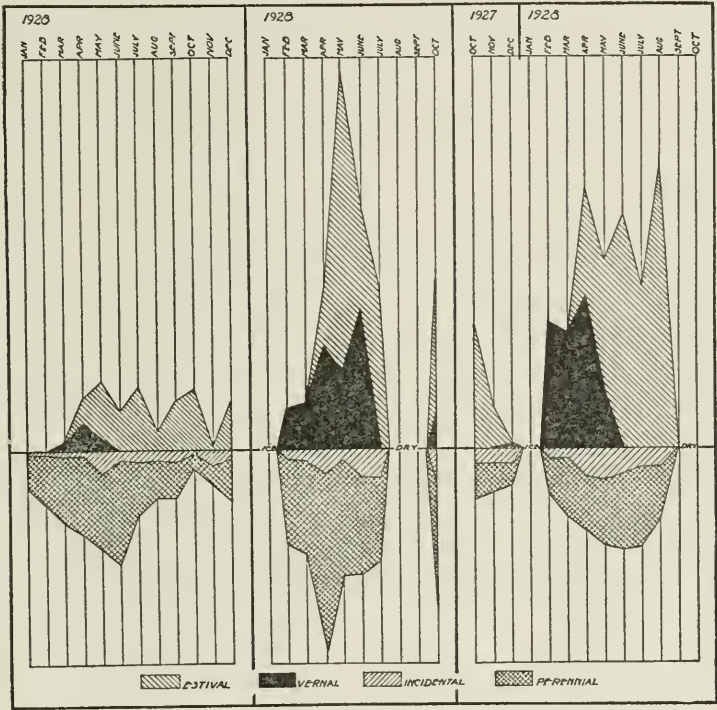


FIGURE 5

FIGURE 6

FIGURE 7

Graphs showing relative volume of principal plankton groups in three bodies of water: FIG. 5, the Sangamon River at Monticello, Illinois, 1928; FIG. 6, a temporary pond near Seymour, Illinois, 1928; FIG. 7, a temporary ox-bow pond north of Urbana, Illinois, 1927 and 1928. (For graphical method, scale, and reduction, see text, page 37.)

In July and August the plankton is usually characterized by the appearance of blue-green algae and the large cladoceran *Leptodora kindtii*. Increasing in abundance, these forms make up a serotinal community.

There is no autumnal community such as has been demonstrated for land by Weese (1924), Smith (1928), and others. The organisms present in the estival and serotinal community usually persist through the autumn

and gradually decline as the water cools, until by the end of December, when the ice forms, the hiemal community develops.

The seasonal communities for the most stable river community studied would be represented in the annual cycle of the plankton of the Illinois River. A study of Kofoid's collections and data for the years 1896, 1897, and 1898 shows that the plankton was composed of various elements (Fig. 4). The perennials, although always present, were not constant in abundance. This group formed the greater bulk of the plankton. Seasonal aspect was caused by the regular periodical appearance of certain organisms which were conspicuous enough to be termed seasonals. The remainder of the plankton was composed of organisms which appeared sporadically (incidentals); because of lack of space they are omitted from the figure.

As this represents the most stable aquatic community studied, the most conspicuous perennials and seasonals are listed here:

<i>Perennial Predominants</i>		Cyclops bicuspidatus
Lysigonium granulatum		Asterionella gracillima
Microcystis aeruginosa		
Pediastrum duplex		<i>Estival Predominants</i>
Diffugia lobostoma		(March to December)
Diffugia globulosa		Closterium acerosum
Trachelomonas volvocina		Euglena oxyuris
Phacus longicauda		Euglena viridis
Codonella cratera		Brachionus angularis
Polyarthra trigla		Filinia longiseta
Brachionus calyciflorus		Asplanchna brightwellii
Brachionus capsuliflorus		Eudorina elegans
Keratella cochlearis		Tintinnidium fluviatilis
Synchaeta stylata		Conochiloides natans
Synchaeta pectinata		Daphnia longispina
Bosmina longirostris		Diaptomus pallidus
		Diaptomus siciloides
<i>Hiemal Predominants</i>		
(December to April)		
Synura uvella		<i>Serotinal Predominants</i>
Stentor coeruleus		(July to September)
		Pedalia mira
<i>Vernal Predominants</i>		Diaphanosoma brachyurum
(February to June)		Moina micrura
Keratella quadrata		Leptodora kindtii
Notholca striata		Euglena acus

Many plankton species are not constant in their seasonal appearance. The late vernal and the estival are difficult to distinguish, for there is a continual arrival of species during the whole period. Often one very abundant species will drop out the following year or will change place

with some other form, so that the limits of the estival are doubtful and need further investigation.

Some of the vernal predominants of the park pond at Decatur, such as *Synchaeta pectinata*, *Brachionus calyciflorus*, *Filinia longiseta*, and *Conochiloides natans*, were distinctly estival predominants in Lake Decatur.

Species of *Diaptomus*, because of their erratic distribution, are very unreliable as seasonal indicators. In the Illinois River and in the park pond at Decatur, *Diaptomus pallidus* appeared regularly as an estival form, but no species of this genus was found in the park pond at Urbana. *Diaptomus siciloides* appeared as an estival form occasionally in the pool of the Sangamon at Decatur and regularly in the collections of Kofoed on the Illinois River, but it never appeared during the four years observations on the park pond at Decatur.

As most of our waters are not stable, considerable shifting is to be expected. Also, immaturity of the communities causes many species to arrive later than they would in a body of older water. The plankton organisms in the writer's collections from the park ponds at Decatur and Urbana and in Kofoed's collections from the Illinois River showed much more regular distribution than the forms in Lake Decatur. The hiemal, early vernal, and serotinal communities are clearly defined by the characteristic organisms mentioned. Bennin (1926) found the annual cycle of the plankton in the Warthe to be divided into four seasonal groups as follows: February to April, May to June, July to September, October to January. These seasonal groups practically coincide with the vernal, estival, serotinal, and hiemal societies described in this paper.

YOUNG STREAMS

In young streams, where plankton does not begin to develop until the water is more than a week old, the only seasonal societies discovered in the plankton is an estival society. For example, a scanty plankton first appeared in the course of the Sangamon River at Monticello, where the age of the water was about 9 days. This plankton was present only from May until October, and was composed of many organisms which are perennial under more stable conditions farther downstream.

TEMPORARY PONDS

Seasonal societies were hard to distinguish in the plankton element of the temporary ponds, where much of the plankton was composed of adventitious forms. No winter plankton existed, because the ponds were generally frozen solid during those months. When the ponds thawed in

February or March, many of the characteristic forms appeared and persisted until the ponds dried up in mid-summer. At this period a vernal socies can be determined by the presence of *Notholca striata*. Often other characteristic forms appeared, such as *Diaptomus sanguineus* and various species of *Eubbranchipus*. Some hiemal species such as *Synura uvella*, which persist through the vernal socies in streams and perennial ponds, always occurred in the vernal socies of the temporary ponds showing that a hiemal socies would be present if it were not for the ice. The vernal forms usually disappeared in May, and except for the summer appearance of chlorophyl-bearing flagellates there were no regular or characteristic species to designate estival or serotinal socies. The ponds were usually dry in August and September, filling again in October. Within two weeks after filling, most of the forms present before drying up were again abundant and remained until the ponds froze in December. In a strict sense, there are no true perennials in these ponds, as all organisms are inactive during winter and mid-summer. The only organisms comparable to perennials are those which are present at all times when the ponds are not dry or frozen.

GLACIAL LAKES

The lack of seasonal data on glacial lakes makes it impossible to describe their seasonal communities definitely. Very deep lakes because of their lower and more uniform temperature throughout the year would not be expected to show much seasonal differentiation. Lake Michigan, because of its relative stability throughout the year, did not show any great seasonal differences in the plankton (Eddy, 1927). There was some indication that seasonal communities may exist in Lake Michigan from the collections made throughout the years 1887-1888 by the Illinois State Laboratory of Natural History. The occurrence of *Daphnia longispina*, *Diaptomus sicilis*, *Dinobryon sertularia*, *Synchaeta stylata*, and *Diaphanosoma brachyurum*, all in great abundance in summer, may indicate an estival or serotinal socies.

A study of the seasonal data of a moderately deep glacial lake as presented by Birge and Juday (1922) shows very few seasonals among the conspicuous or predominant planktonts of Lake Mendota. Most of the predominants listed are perennials, and this may be due to the fact that the seasonal conditions of such a lake do not have as wide a range as those of smaller and shallower lakes. Vernal and autumnal forms are chiefly diatoms which appear and increase after the overturn of the thermocline. Estival predominants or prevalents are chiefly algae, particularly species of *Anabaena*, *Lyngbia*, and *Microcystis*.

PLANKTON DEVELOPMENT AND RELATED FACTORS

The development of the plankton communities studied differs from that of terrestrial communities in that it is a steady progression rather than a succession. The water of streams is motile and to a great extent carries the pelagic community along as it flows from one stage of river conditions to another. Consequently, at any given point in the stream, the plankton is constantly shifting downward, never containing the same set of individuals for any long period of time. This means that at any fixed point, as the water flows downstream, there must be a continual production and replacement of plankton. In the course of the stream, as soon as seasonal and other conditions permit, the first plankton appears as a scanty community; as the water proceeds, this community continues to develop, adding species, all of which, if conditions remain favorable, reproduce and increase in numbers, until eventually the community approaches that of a stable stream. This is a progression of organisms rather than a succession in which one aggregation is succeeded by another entirely different.

At any given point in a stream, it is apparent that plankton develops by a series of progressive stages rather than by a succession of forms. True succession in water, in so far as plankton is concerned, depends partly on the point of view as to what constitutes an aquatic habitat. If the moving stream is considered as a continually moving habitat, always created anew at the source and continually moving downstream, then it is conceivable that true plankton succession might occur under certain conditions. Such conditions might exist in a stream, such as the Mississippi, which, flowing a great distance from north to south, passes through several sets of climatic conditions. Shifts in the climatic factors, particularly temperature, may cause some predominants to drop out and to be replaced by others, thus constituting a true succession. Further study may show, however, that such a stream passes from one aquatic climax to another.

On the other hand, if the habitat is considered as fixed along with the bottom (and there is some evidence to support this), then the development of plankton would not be in the course of the stream but at any fixed point, and here it seems to be a progression rather than a succession of predominants. Due to the fact that most streams pass through various stages of size and fall in development, it is necessary to study similar stages, found at present in the upper course, in order to determine the past development at any fixed point. However, such a series of longitudinal studies should be within the same climatic area.

In Lake Decatur as an example of newly formed bodies of water, plankton development year after year was found to be a steady progression toward a stable community. There was a progression of forms from the time the lake was first studied in 1923, when it was one year old, until 1929, when the last collections were made (Table 19). Each year a few additional species appeared, and nearly all the species showed a tendency to increase in abundance as the lake became older. No species actually disappeared, although *Pleodorina illinoisensis*, noticeably abundant in the early summer of 1923, was never found to be abundant in following years.

Plankton development is comparable to the invasion of barren areas by terrestrial forms. In waters where the plankton appears in only scanty numbers and for only a part of the year, it may be compared to plants in the desert which spring up during the rainy season. No other pelagic organisms previously occupied the waters of the streams studied, and there is no evidence that any plankton forms were actually succeeded by other planktons. Therefore, in streams, there is no evidence of succession of plankton communities comparable to the usual succession of terrestrial communities. The only such succession was that found in the pond sere, where the water was stationary and the trend was toward a terrestrial climax. The plankton of perennial ponds containing stable-river predominants was succeeded, as the ponds approached littoral conditions, by temporary-pond plankton characterized by temporary-pond predominants. As this succession is toward a terrestrial climax, it has little significance in the development of plankton communities.

The invasion of new waters by plankton is dependent upon certain conditions which hasten or retard the development of the plankton. The most variable factors in all the waters studied by the writer were age, temperature, turbidity, and level of the water. Dissolved oxygen, hydrogen-ion concentration, and light, although varying more or less in the different seasons, were always well within the limits of plankton requirements. Other chemical factors, though not yet accurately determined to any extent, probably play an important part, particularly in relation to the food supply.

AGE OF WATER

An opportunity to study the development of plankton in relation to age of water in the course of a stream was found when the Sangamon was dammed at Decatur in 1922. The old river channel from the source to the collecting station at Lost Bridge was 89 miles long. The formation of the lake retarded the waters so that they were many days older when they reached the station than before the dam was built. By computing the age of the water at different points in the lake and stream above, and

by tracing the stage of development of the plankton, it was possible to secure data on the age of the water at which plankton production started and the age at which it became heavy.

The source of the Sangamon River is in a group of springs and ditches where the stream may be first distinguished 6 miles northwest of Fisher, Illinois. Throughout the course of the Sangamon from its source to the head of the lake at Decatur, there are constant additions from tributaries and springs. There is no information as to the exact amount of water added, but it probably is approximately as much as the water already in the stream at Fisher. Consequently, the actual age of all the water at a given point was impossible to determine accurately. One great difficulty lay in determining the velocity at which the water flowed through the lake. Because of the irregular contour, only approximate results could be secured. The lake extends 10 miles above the collecting station and contains approximately 33 times the volume of water formerly in the old river channel. Hence, the lake is theoretically equivalent to 330 miles of river channel. It is practically impossible to measure the current as in a normal river channel, because it is perceptible only in the narrowest places, where bridges have been constructed. No doubt, the water in the center of the lake moves faster than that near the shores, but because of the bends and headlands, there is considerable intermingling of shore and center waters. This was demonstrated in repeated collections in cross-sections where the only appreciable differences in the plankton content were found in the vegetation close to the shore line. The winds cause considerable wave action on the lake and serve as a factor in keeping the waters well circulated. The river channel extends for 79 miles above the head of the lake to its source. The total distance from the source to the collecting station at Lost Bridge was equivalent to 409 miles of river channel. As the velocity could not be measured in the lake it was necessary to assume that it was the same as that of the river above the lake. This was reasonable, as no appreciable difference could be found in the velocity of the river from Mahomet to the head of the lake or in the river below the lake. The velocity was measured semi-monthly during 1928 at Mahomet and Monticello. In Table 17, there is some discrepancy in the averaged gage readings and velocities because the gage readings were made daily and the velocities only semi-monthly. Occasional measurements were taken at Cerro Gordo and at Coulter's Mill just above the lake. Broomstock floats were used, and care was taken to select quiet days when there was no wind interference.

During flood stages in February, 1928, the water in the river just above the lake reached the greatest velocity recorded, 9,000 feet per

hour, and the age of the water at the Lost Bridge station on the lake was computed at 9 days and 21 hours. Usually, however, it took much longer to reach this station. The longest period, obtained by similar calculations, was 173 days and 20 hours on October 1, 1928, when the velocity in the river was 511 feet per hour. During periods of normal level, a well-developed plankton first appeared in March at Rhea's Bridge five miles below the head of the lake (Table 17). At the head of the lake only a scanty plankton occurred at the low-water stages. At Monticello from May to October, with a high temperature and low-water stage, a

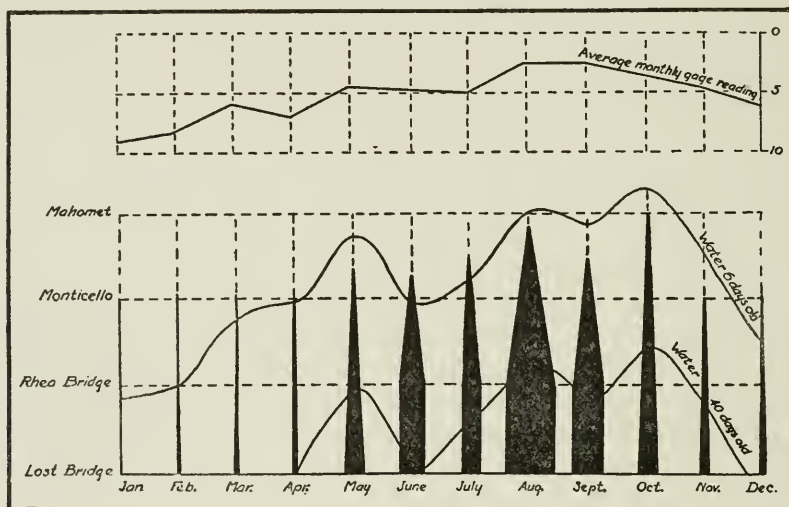


FIGURE 8

Graphs showing relation between age of water and volume of plankton at four collecting stations on the Sangamon River, 1928. Government gage readings at Monticello are plotted above the graphs of relative volume of the plankton in each month. On the same diagram are plotted two curves showing for each month the point in the stream where the water had an estimated average age of 6 days and of 40 days, respectively.

few plankton organisms were found in water averaging from 6 to 19 days old. The water was nearly always at least 20 days old before plankton organisms appeared in any abundance.

Table 18, showing the progression of organisms in the river from Mahomet to Lost Bridge, was based on the June collections of 1928. Fig. 8 shows graphically the relative volume of the plankton in the Sangamon River each month between Lost Bridge and Monticello. The age of the water and the gage reading have been plotted above showing the correlation with the distribution of plankton. Bottom diatoms and

protozoans composed most of the catch in the plankton net at Mahomet. These forms decreased as the water proceeded downward, and in about 6 days a few planktons appeared at Monticello. When the water had reached Rhea's Bridge, about 20 days from the source, all these forms had increased in abundance, and seven new forms had appeared. At Lost Bridge, about 40 days from the source, thirteen more forms appeared, and nearly all had increased in abundance. In other months, there was some difference in the predominant species which appeared at Monticello and Rhea's Bridge, but they were never many or abundant.

According to Kofoed (1903), the Illinois River in low stage replaces its water between LaSalle and the mouth about every 23 days. The water in general at LaSalle may be safely assumed to be already about three weeks old. Therefore, most of the water at Havana, where Kofoed found abundant plankton, was at least 12 to 15 days old or more, even at flood stage, when the velocity was 9,000 feet per hour.

Schroder (1897), working on the phytoplankton of the Oder River, first described the relation of plankton to the flow of water by stating that the amount of plankton in running water of the river is in inverse proportion to the slope of the river. Consequently, as a stream approaches maturity, i.e., as it approaches a base level and its current becomes slower, there should be a proportional increase in plankton production, and this condition of maturity may be hastened by artificially retarding the waters. Similarly, the farther a stream flows from its source and the more stable its conditions tend to become, the more developed is the plankton element of the pelagic society. Kofoed from his work on the Illinois River concluded that the quantity of the plankton was, within certain limits, directly proportional to the age of the water.

TEMPERATURE

The fluctuation of river temperature constitutes one of the most marked evidences of climatic changes. The temperature runs through the same general annual cycle year after year with only minor or local variations. Temperature probably affects planktons by retarding or accelerating their growth and reproduction (Kofoed, 1903), and it is partly responsible for the seasonal fluctuations in their abundance. Temperature also affects planktons by causing variations in viscosity and density (Wesenberg-Lund, 1908). In the tropics (Van Oye, 1926) where a more uniform temperature prevails throughout the year, temperature does not play an important part as a seasonal factor in plankton abundance.

Water communities do not exhibit the extreme seasonal fluctuations to which land communities are subject. The seasonal change is gradual, with but little fluctuation. The waters of large streams, lakes, and ponds

studied by the writer did not show as much daily fluctuation in temperature as was found in the temperature of the air. The deeper the water, the more uniform is the temperature from day to day. In Lake Michigan the water cooled more slowly than the air in the autumn and consequently was generally warmer; in the spring the reverse was true. Large bodies of water reach freezing temperature on the surface only, and plankton organisms underneath live at a temperature usually higher than that at which organisms live on land. Many species, such as the hiemal and vernal seasonals, show temperature preferences by becoming scarce or rare as the temperature passes certain limits. Others, chiefly the perennials, have a large degree of tolerance for temperature extremes, although they are seldom as abundant at the lower temperatures. The rate of fresh-water plankton reproduction—and consequently the abundance—at different seasons in the same body of water varies directly with the temperature. Similarly, plankton content varies in bodies of water differing in temperature, as will be discussed later. In the course of any given stream where there is little climatic variation from the source to the mouth, temperature differences are too slight to have much influence on the development of the plankton.

VELOCITY AND WATER LEVEL

Velocity of current is one of the important factors directly influencing plankton production. Water level, in itself, is not so important in regard to plankton as is the corresponding velocity. Velocity and water level are closely related; as the water level rises the velocity increases. At any given point in a stream, fluctuations of velocity result from fluctuations in water level. Velocity is usually higher in young streams, and the consequent erosion may increase the turbidity and hence reduce the intensity of light. In older streams where velocity is usually lower, the turbidity may decrease and the intensity of light increase. Turbidity, by increasing as the level is raised, actually moves the point of plankton production farther downstream. Kofoid (1903) observed that streams with great velocity usually have more phytoplanktonts than zooplanktonts, and for this he advanced the explanation that the swift current prevents the zooplanktonts from feeding but does not have so much effect on the assimilation processes of the phytoplanktonts. Allen (1920) in his studies on the San Joaquin River concluded that water currents above a very moderate speed are inimical to plankton production. The writer has observed that small streams with a swift current, draining lakes or ponds containing an abundant plankton, carry little plankton themselves, and that what little they do carry comes originally from the source body

and tends to decrease rather than increase. Velocity is one of the important factors controlling the age of the water and corresponding conditions of stability necessary for the production of plankton. Velocity, thus, largely determines the point in a stream at which plankton production starts, and this point fluctuates up or downstream according to the velocity of the current, being farthest downstream when the velocity is highest and farthest upstream when the velocity is lowest.

TURBIDITY

Turbidity, an important factor in reducing light and hindering the movements of many planktons, is partly controlled by velocity of current, as previously stated. When the current is reduced as the stream approaches stability, there is more tendency for the suspended silt to settle to the bottom. When the turbidity was high in the Sangamon above Lake Decatur, there was a gradual reduction as the water travelled through the lake until at Lost Bridge the turbidity was seldom noticeable, and the plankton was more abundant there than above. In all the streams studied, the turbidity due to suspended silt was highest at the flood stages of spring and summer and lowest in winter when the streams were at normal level. In summer, when the current was usually slow and there was very little suspended silt in the water, a noticeable turbidity was often caused by the increased plankton content. The turbidity in the park ponds was usually high in summer, often giving the water a very muddy appearance although it was due entirely to the heavy plankton content. Suspended silt was practically absent from these ponds because of the lack of disturbing current. In all waters a high turbidity due to suspended silt retards plankton development, and the velocity and other conditions must be such as to reduce this turbidity to proper value before plankton production can be heavy.

LIGHT

Light, another important factor in plankton existence, especially in regard to the chlorophyl-bearing forms, has long been regarded as one of the factors limiting the vertical distribution of plankton. Aside from the differences produced by turbidity, depth, and seasons, light conditions were normal or about the same in most of the waters studied. The length of days in different seasons probably influences plankton abundance and may influence the appearance of seasonal predominants, particularly algae. Kofoid (1903) and Allen (1920) both observed indications of "lunar" pulses in the plankton and explained them on the basis of an increased amount of lunar light. The measurable differences, how-

ever, are too slight to be of much significance. In winter the ice reduces the amount of light in the water and no doubt is a factor in lowering plankton production. Intensity of light is reduced in the younger streams because of the silt produced by erosion. In more stable streams the settling out of the silt allows increased penetration of light and no doubt plays a very considerable, though as yet undetermined, part in the development of plankton.

CHEMICAL FACTORS

Hydrogen-ion concentration was not an important factor in any water where plankton development was studied. The pH value of natural waters is indicative chiefly of relative acidity, which in turn is largely due to the relative amount of dissolved carbon dioxide, so that pH readings may be regarded as reflecting indirectly the CO_2 content (Birge and Juday, 1911; Shelford, 1929). The pH value of the water studied by the writer generally ranged from 7.8 in summer to 6.6 in winter, but the fluctuations were not always seasonal. In the park pond at Decatur and in other waters, most predominant planktons were found abundantly at all pH values within the range stated above, indicating that this range was well within the limits of tolerance for most of the planktons studied. High hydrogen-ion concentration, such as pH 4.0, influences many planktons, but none of the natural waters studied approached such an extreme value, except in swamps and bogs where some of the non-acid rotifers were absent. Harring and Myers (1928) note the absence of certain plankton rotifers from acid waters and state that the pH range for rotifers is as a rule from 2 to 3 units pH. No marked difference in pH values occurred in the waters of the Sangamon River at the points studied for plankton development, and evidently this factor did not play any part in plankton production in this stream.

The dissolved oxygen in the waters studied, as previously mentioned, was never found to be below the requirements of the plankton. Usually it ran higher in the colder months, since the water can hold more gases in solution at lower temperatures. As the plankton, in general, was most abundant in summer when the dissolved oxygen content was lowest, it seems that the dissolved oxygen played little part in seasonal distribution in the shallow waters. Although the writer made no studies on oxygen conditions in deep lakes in the different seasons, these conditions no doubt have more significance there, in regard to seasonal distribution, than in shallow lakes. Birge and Juday (1911) found that the dissolved oxygen content in the surface waters of Lake Mendota was sufficient at all times of the year, but in the deeper waters it was often insufficient, because of the seasonal stratification. In the study of the development of plankton

in the Sangamon River no marked differences were found in the amount of dissolved oxygen at different points in the stream, and it is reasonable to believe that this factor, being sufficient for ordinary requirements, had little influence on the development of the plankton.

Very few data are available on the dissolved salts and other substances in the waters studied. The samples that were analyzed indicated that there were considerable differences. For example, the waters of the park ponds contained more than 10 times as much chlorine in the form of chlorides as did the Sangamon River. Griffith (1923) has shown that waters free from calcium carbonate produce more desmids than waters bearing this salt. In December, 1928, the Illinois State Water Survey, at the writer's request, made chemical analyses of samples from two stations on the Sangamon River and from the park ponds at Decatur and Urbana, with results as shown below in terms of chlorine in chlorides, expressed in parts per million:

Sangamon River at Monticello.....	2
Lake Decatur at Lost Bridge.....	4
Decatur Park Pond.....	30
Urbana Park Pond.....	23

The relatively great amounts of dissolved salts indicated by these analyses of the pond waters may be partly responsible for the heavier plankton in these ponds. In general, it is probable that chemical factors play an essential part in development of plankton. Water flowing down a stream-bed has increasing opportunities to dissolve both organic and inorganic substances, some of which no doubt are made available as food to plankton organisms by bacterial action. Griffith (1923) concluded that the presence of plankton depends on the occurrence of suspended organic matter, the decomposition of which provides necessary food materials, and that the amount of plankton depends on the amount of products of fermentation. Pearsall (1922) showed that the plankton increases when there is an increase in certain salts and organic matter. This is in harmony with the observed fact that plankton is more abundant in natural waters of some age, which are obviously more suitable for plankton occupation than juvenile waters near their sources. The determination of the separate and combined effects of such factors is an indispensable step in understanding the phenomena of plankton production and constitutes a very important field for future investigation.

BIOLOGICAL FACTORS

Plankton development requires, first, that the water must be old enough to allow time for the planktons to grow and reproduce, and

that in streams the current must be slow enough to enable the zooplanktonts to feed (Kofoid, 1903). Little is known about the rate of reproduction or length of time necessary for the embryological development of plankton organisms, but these biological factors certainly play some part in determining the point at which any given organisms appear in the course of a stream. Food requirements are at present little understood. Food may not be as important a factor in the distribution of plankton organisms as it is in the distribution of some terrestrial forms. Phytoplanktonts and chlorophyl-bearing zooplanktonts, for example, by utilizing raw materials, are less dependent on the food-factor than are the other zooplanktonts. Even the latter, moreover, are often found where there is little evidence of the phytoplanktonts on which it has been assumed that they feed. This indicates that they, too, may utilize other materials. In view of the present status of the question regarding the utilization of the organic content of waters by plankton organisms (Birge and Juday, 1926), the writer prefers to leave this matter for further investigation.

INTERRELATIONS OF FACTORS

Hydrogen ion concentration and the dissolved oxygen content being usually favorable, as in the waters studied, the important factors observed in the production of plankton are temperature and velocity of the water. Temperature controls the rate of vital processes involved in growth and reproduction. Velocity of current is a factor in age of water and must allow time for the organisms to develop and multiply and possibly for suitable conditions of nutrition to be established. Slow current also permits the zooplanktonts to feed more freely. As the velocity decreases, the turbidity is lowered and more light penetrates the water to greater depths. When all these conditions are favorable, plankton production conceivably may continue to increase until it automatically checks itself, not only by exhausting the food supply, but also by causing such a high turbidity that the amount of light penetrating the water is insufficient for further growth and reproduction. This hypothesis would explain such facts as were observed in the park pond at Decatur, where extreme turbidity was caused by heavy zooplankton production and the algae, being most dependent on abundant light, were scarce. Juday and Wagner (1909) have suggested that plankton may become so abundant that it becomes detrimental to other organisms by the consumption of oxygen through decay. Also it is conceivable that the oxygen content might be depleted by the demand of super-abundant plankton to the point when it might form a check on the development of the plankton.

GEOGRAPHICAL DISTRIBUTION AND
ECOLOGICAL CLASSIFICATION

Very little is known about the plankton organisms in many parts of the world. In vast areas, particularly South America and Australia, our information is limited to a few reports on several groups of plankton organisms. Daday's reports on some of the plankton organisms from Patagonia (1902) and on the fresh-water organisms of Paraguay (1905) (Lemmermann, 1910) include many forms which are predominant, or prevalent, in the waters studied in this paper. Juday (1915), in a study of some lakes in Central America, found many species which are common here. West (1909), on algae, and Playfair (1912 and 1919), on plankton and dinoflagellates, show that the plankton of Australian waters contains many of the same species in these groups as found elsewhere. Similar results are shown in the papers of Daday (1907), West (1907), and Cunningham (1920) on groups of plankton organisms from African lakes. Van Oye (1926) found a heavy stream plankton in the Ruki in Belgian Congo, which contained many of our common river predominants. Pernod and Schröter (1924) have shown that many of our predominant species of Cladocera are distributed in eastern and southern Asia. The predominants reported by Lemmermann (1907a) from the Yang-Tse-Kiang in China, although differing somewhat in species, are similar to those found in the relatively stable streams studied in this paper. Zacharias (1898, 1898a, and 1909), Lemmermann (1907b), and many workers since have contributed extensive data on the plankton of central European waters. Behning and his associates have done likewise for the Volga and its tributaries, showing the wide distribution of many of the predominants studied in this paper and the limited distribution of other species, particularly those cladocerans and copepods which are not found in America.

Wesenberg-Lund (1908), in an extensive geographical classification of plankton, shows that many species are cosmopolitan and others are strictly local. Species scattered commonly throughout the lakes of the arctic, temperate, and tropical regions include many Bacillariaceae, Cyanophyceae, Chlorophyceae, and Flagellata. Rotifers are especially conspicuous and include *Keratella cochlearis*, *Keratella quadrata*, *Polarthra trigla*, *Asplanchna brightwellii*, *Triarthra longiseta*, species of the genus *Brachionus*, and *Pedalia mira*. Other conspicuous forms are *Daphnia longispina*, *Bosmina longirostris*, *Chydorus sphaericus*, *Cyclops viridis*, and *Cyclops leuckarti*. The species of the Diaptomidae especially show differentiation in different regions, but the cosmopolitan species were all found to be predominants in the waters studied in this paper.

All the conclusions reached in this paper in regard to communities are based on plankton evidence only. The question whether various aquatic communities are of formational or associational rank, cannot be answered definitely until the bottom organisms and fishes are studied in relation to communities throughout large areas. If the cosmopolitan predominants in the plankton were accepted as stenoeious species, they would indicate that there is but one fresh-water association in the world. Inasmuch, however, as the fishes—many of which are dominant—and also the bottom organisms—some of which may be dominant—do not show this wide-spread distribution, it may be better to consider the predominant fishes and bottom organisms as stenoeious species determining associational boundaries. Although without much evidence, the writer is inclined to believe that a study of the latter species will show that they define a number of aquatic associations in various parts of the world. Some investigators may consider the cosmopolitan planktonts as comparable to the wide-spread soil bacteria, algae, and protozoans (Sandon, 1927). Studies of these minor terrestrial forms, to determine their community distribution and community structure, may show that they occupy the same status on land as is occupied by plankton in water.

In view of the results of this investigation it is to be expected, in general, that an abundant and relatively permanent plankton should occur in any sluggish stream which presents the proper conditions of size, flow, and fluctuation, the other factors being favorable as in all the bodies of water studied. Such streams are:

- 1.—Streams in which natural obstructions render the current slow, as in the Mississippi River where Lake Pepin is formed by the delta of the Chippewa River.

- 2.—Streams with little fall and slow current, resulting from the occupation of ancient and well-worn preglacial channels, such as the Illinois River throughout most of its course.

- 3.—Streams flowing into the sea and practically at base level throughout most of their course, so that conditions are almost as stable as in large lakes.

On the other hand, streams which are at base level near their mouth only, as is the case of the Mississippi, cannot maintain a heavy plankton because the conditions in the upper part are such as to cause a heavy discharge of silt which is detrimental to plankton.

A summary of the predominant or prevalent species in the various types of waters studied is given in Table 20, showing that there are, in general, four types of plankton communities in the upper Mississippi Valley, which may be distinguished as follows:

1.—In rivers and related waters exhibiting some degree of stability, the conspicuous predominants are seven species of rotifers (four of which belong to the genus *Brachionus*, two to *Synchaeta*, and one to *Filinia*) and the cladoceran *Moina micrura*. These with other predominants characterize the pelagic society of stable rivers and the societies of related ponds and shallow lakes. In younger streams or wherever the conditions are less stable, the society is characterized by the same species, but to a lesser degree; that is, they are not as abundant and may not all be present at the same time.

2.—In temporary ponds and littoral parts of stable waters with vegetation, the society is characterized by the copepod *Cyclops serrulatus* and the cladocerans *Camptocercus rectirostris* and several species of *Simonecephalus*. These predominants, together with other characteristic species, such as *Daphnia pulex*, *Moina brachiata*, and bottom rotifers of the genera *Monostyla* and *Lepadella*, may not all be present in a single collection, but they will appear often enough in a series of collections to give a characteristic aspect to the plankton.

3.—In deep glacial lakes the society is characterized by predominants such as the rotifer *Notholca longispina*, the copepods *Diaptomus minutus* and *Epischura lacustris*, the cladocerans *Daphnia retrocurva* and *Bosmina longispina*, and the diatom *Striatella fenestrata*. At least three of these, and often all four, appeared in every collection examined by the writer.

4.—In moderately deep and shallow glacial lakes the pelagic society is characterized by the copepod *Diaptomus oregonensis* and by abundant populations of pelagic diatoms and blue-green algae. The predominants characteristic of deeper glacial lakes are absent or scarce, and the plankton more nearly resembles that of stable rivers.

Analysis of the plankton of Russian waters as described by Behning (1913, 1921, 1926) and of many other European waters as described by a large number of investigators in the past forty years, shows these same general groups of plankton communities characterized by the same predominants. Certain predominants, such as *Cyclops viridis*, *Cyclops bicuspidatus*, *Daphnia longispina*, *Notholca striata*, *Keratella cochlearis*, and *Polyarthra trigla*, are common in all three types of plankton communities. Other predominants, *Pediastrum duplex*, *Diaphanosoma brachyurum*, and *Codonella cratera*, are most abundant in stable rivers and related waters, but are also found in small numbers in other communities. All the predominants mentioned with the exception of the copepods have been found by the writer in plankton collections from similar bodies of water in many parts of the United States.

Fresh-water plankton should be classified ecologically as the pelagic stratal society or societies of the community of a stream or lake. All the plankton communities studied by the writer showed a common ecological relationship by virtue of their possession of common predominants (Table 21), some of which are seasonals and other perennials, and by virtue of their development from common or related sources. Consequently, these plankton communities are considered as belonging to an

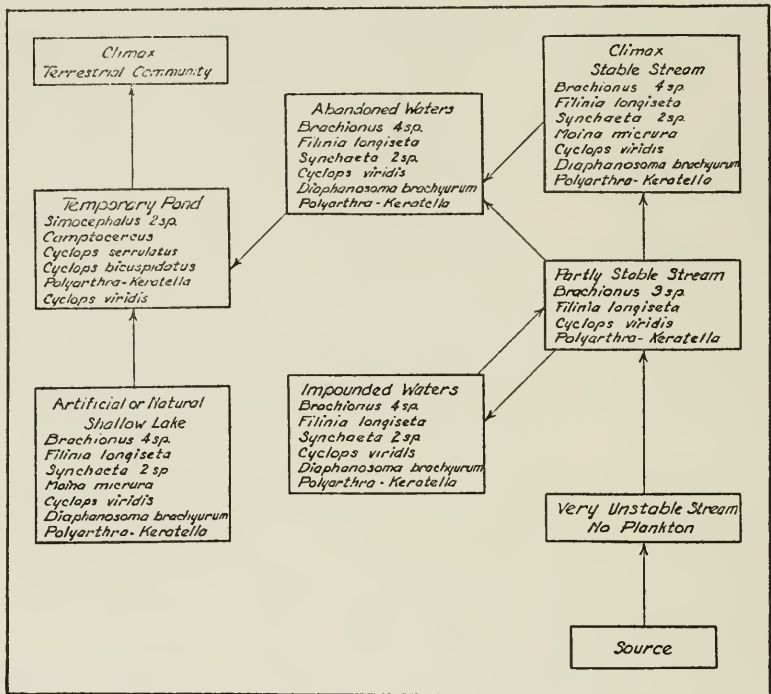


FIGURE 9

Diagram showing developmental relations and general trend of plankton communities in the region of Illinois, as characterized by some of their common predominants.

association, the climax of which is the stable-stream community. Communities other than those of stable streams either are developing toward this climax or, if they occupy abandoned areas of streams or lakes, are developing toward a terrestrial climax (Fig. 9). The Plankton of a community which is not mature, therefore, must be designated as a pelagic stratal societies rather than a society, since the latter term should be applied only to the plankton of the stable-stream community.

SUMMARY

The present study, based on more than 2,000 collections of plankton from streams, lakes, and ponds (mostly in the United States), has shown that the plankton element of fresh-water communities consists of organisms whose behavior is comparable in certain respects to that of the organisms of terrestrial communities. Some species which are conspicuous or abundant may be called predominants or prevalents, in the same sense as these terms are used for the abundant organisms of terrestrial communities. Some predominants are perennials and others seasonals. Some predominants are common in all kinds of relatively stable fresh-water communities and indicate an associational and formation-like structure comparable to that of terrestrial associations and formations, in which the predominants are of two classes, those which characterize the particular association and those which characterize the formation and serve as binding species.

In all the streams studied the plankton element gave evidence that stream communities—inasmuch as they belong to an aquatic association, the climax of which is a stable-river community—should be considered as separate from terrestrial communities.

Some predominants which are seasonal in the early stages of plankton development in a stream become perennials when the stream presents more stable conditions throughout the year.

There is a progressive development of the plankton element in streams comparable to the invasion of the barren area by terrestrial communities. This begins with the first evidence of stable conditions in the course of the stream in summer. Downstream, as the conditions become more stable, there is an increase in the number of species and the abundance of each. The most mature communities studied were found to contain about forty predominant organisms. Apparently, the number of perennials increases as the climax is approached.

The predominants in perennial ponds and shallow lakes are the same as the predominants in stable rivers. Many such ponds or lakes are abandoned parts of streams, and others which are not in any way connected with streams but contain similar predominants, may be considered as natural or artificial reproductions of abandoned parts of streams. The communities of these bodies of water are retrograding from the aquatic climax and are at some stage of succession towards a terrestrial climax and, hence, properly belong to a terrestrial association.

The last aquatic stage in the succession of pond communities toward a terrestrial climax is found in temporary ponds which contain a scanty plankton characterized by several predominants partly littoral in origin.

Three seasonal groups, or socies—hiemal, vernal, and serotinal—and possibly a fourth, estival, can be distinguished in the plankton of shallow lakes and streams of Illinois and are characterized respectively by seasonal predominants.

The important factors influencing the development of plankton are age of water (i.e., distance from source \div velocity), temperature, and turbidity. In the streams studied, other factors such as light, dissolved oxygen, and hydrogen ion concentration seemed to be always sufficient to meet the requirements of the plankton. Observations on the plankton of water of different ages showed that, all other factors being favorable, a few plankton organisms usually appeared in water 6-10 days from its source, while an abundant plankton appeared in water 20 days or more from its source.

In the bodies of water studied, there are, in general, four types of plankton society or socies which may be characterized by their predominants as follows:

1.—Rivers and related waters exhibiting some degree of stability: four species of *Brachionus*, two of *Synchaeta*, *Filinia longiseta*, and *Moina micrura*.

2.—Deep lakes: *Notholca longispina*, *Striatella fenestrata*, *Daphnia retrocurva*, *Bosmina longispina*, and *Diaptomus minutus*.¹

3.—Temporary ponds: *Cyclops serrulatus*, *Camptocercus rectirostris*, and two species of *Simocephalus*.

4.—Moderately deep and shallow glacial lakes: *Diaptomus oregonensis*, pelagic diatoms, and blue-green algae.

If the vagile elements of the pelagic portion of the community and the bottom society or socies show similar differences in various areas, these aquatic communities are of associational rank.

CHECK LIST OF NAMES OF SPECIES

Key: Al=Algae; Cl=Cladocera; Co=Copepoda; Pr=Protozoa; Ro=Rotatoria.

Acroperus harpae Baird.....Cl	Daphnia longispina var. hyalina
Alona affinis (Leydig).....Cl	Leydig.....Cl
Anabaena circinalis (Kütz.) Hansg..Al	Daphnia pulex (de Geer).....Cl
Anabaena spiroides Lemm.....Al	Daphnia retrocurva Forbes.....Cl
Anuraea aculeata Ehr.=Keratella	Diaphanosoma brachyurum (Liéven).Cl
quadrata (O.F.M.).....Ro	Diaphanosoma leuchtenbergianum
Anuraea cochlearis Gosse = Kera-	Fischer.....Cl
tella cochlearis (Gosse).....Ro	Diaptomus ashlandi Marsh.....Co
Aphanizomenon flos-aquae (Linn.)	Diaptomus gracilis Sars.....Co
Ralfs.....Al	Diaptomus graciloides Sars.....Co
Aphanocapsa sp.....Al	Diaptomus leptopus Forbes.....Co
Arcella vulgaris Ehr.....Pr	Diaptomus minutus Lillje.....Co
Asplanchna brightwellii Gosse.....Ro	Diaptomus oregonensis Lillje.....Co
Asplanchna priodonta Gosse.....Ro	Diaptomus pallidus Herrick.....Co
Asterionella gracillima Heiberg.....Al	Diaptomus sanguineus Forbes.....Co
Bosmina coregoni Norman & Brady..Cl	Diaptomus shoshone Forbes.....Co
Bosmina longirostris (O.F.M.).....Cl	Diaptomus sicilis Forbes.....Co
Bosmina longispina Leydig.....Cl	Diaptomus siciloides Lillje.....Co
Brachionus angularis Gosse.....Ro	Diaptomus vulgaris Schmeil.....Co
Brachionus budapestinensis Daday..Ro	Diffugia acuminata Ehr.....Pr
Brachionus calyciflorus Pallas.....Ro	Diffugia globulosa Duj.....Pr
Brachionus capsuliflorus Pallas.....Ro	Diffugia lobostoma Leidy.....Pr
Brachionus havanaensis Rousset..Ro	Diffugia pyriformis Perty.....Pr
Brachionus patulus O.F.M.....Ro	Dinobryon sertularia Ehr.....Pr
Camptocercus rectirostris Schoedler..Cl	Epischura lacustris Forbes.....Co
Canthocamptus sp.....Co	Epischura nevadensis Lillje.....Co
Centropxyxis aculeata Stein.....Pr	Eudorina elegans Ehr.....Pr
Ceratioides hirundinella O.F.M.....Pr	Euglena acus Ehr.....Pr
Ceriodaphnia lacustris Birge.....Cl	Euglena acutissima Lemm.....Pr
Ceriodaphnia pulchella Sars.....Cl	Euglena oxyuris Schmarda.....Pr
Chilodon cucullus O.F.M.....Pr	Euglena spiroides Lemm.....Pr
Chroococcus sp.....Al	Euglena viridis Ehr.....Pr
Chydorus sphaericus (O.F.M.).....Cl	Filinia longiseta (Ehr.).....Ro
Closterium acerosum (Schrk.) Ehr..Al	Fragilaria crotonensis (Edw.) Kitton..Al
Closterium moniliferum (Bory) Ehr..Al	Glenodinium sp.....Pr
Codonella cratera (Leidy) Vorce....Pr	Gyrosigma acuminatum (Kütz.)Cl...Al
Coelosphaerium naegelianum Unger..Al	Keratella cochlearis (Gosse).....Ro
Coleps hirtus Ehr.....Pr	Keratella quadrata (O.F.M.).....Ro
Conochiloides natans (Sel.).....Ro	Lecane unguolata (Gosse).....Ro
Conochilus volvox Ehr.....Ro	Lecquereusia epistomium Penard....Pr
Cosmarium spp.....Al	Lepadella acuminata (Ehr.).....Ro
Crucigenia spp.....Al	Leptodora kindtii (Focke).....Cl
Cyclops bicuspidatus Claus.....Co	Limnocalanus macrurus Sars.....Co
Cyclops leuckarti Claus.....Co	Lysiginium (Melosira) granulatum
Cyclops oithonoides Sars.....Co	(Ehr.) Kuntze.....Al
Cyclops serrulatus Fischer.....Co	Lysiginium (Melosira) varians
Cyclops strenuus Fischer.....Co	(Ag.).....Al
Cyclops viridis Jurine.....Co	Microcystis aeruginosa Kutz.....Al
Daphnia longispina (O.F.M.).....Cl	Moina brachiata (Jurine).....Cl
Daphnia longispina var. cucullata	Moina micrura Kurz.....Cl
Sars.....Cl	Monostyla lunaris Ehr.....Ro

Navicula spp.....	Al	Simocephalus vetulus (O.F.M.).....	Cl
Nitzschia sigmoidea (Nitz.) W. Sm..	Al	Sphinctocystis eliptica (Kütz.) Kuntze..	Al
Notholca longispina Kellicott.....	Ro	Sphinctocystis librilis (Ehr.) Hass....	Al
Notholca striata (O.F.M.).....	Ro	Staurostrum spp.....	Al
Oscillatoria spp.....	Al	Stentor Coeruleus Ehr.....	Pr
Paramoecium bursaria Ehr.....	Pr	Striatella fenestrata (Kütz.).....	Al
Pedalia mira (Hudson).....	Ro	Strombidum sp.....	Pr
Pediastrum duplex Meyen.....	Al	Surirella robusta Ehr.....	Al
Peridinium spp.....	Pr	Synchaeta pectinata Ehr.....	Ro
Peridinium tabulatum (Ehr.).....	Pr	Synchaeta stylata Wierz.....	Ro
Phacus acuminata Stokes.....	Pr	Synedra acus (Kütz.) Gun.....	Al
Phacus longicauda (Ehr.) Duj.....	Pr	Synedra ulna (Nitz.) Ehr.....	Al
Phacus pleuronectes (O.F.M.) Duj..	Pr	Synura uvella Ehr.....	Pr
Platylas quadricornis (Ehr.).....	Ro	Testudinella patina (Hermann)...	Ro
Pleodorina illinoisensis Kofoid.....	Pr	Tintinnidium fluviatilis Stein.....	Pr
Pleuroxus denticulatus Birge.....	Cl	Trachelomonas hispida (Perty)	
Polyarthra platyptera Ehr. = Poly-		Stein.....	Pr
arthra trigla Ehr.....	Ro	Trachelomonas volvocina Ehr.....	Pr
Polyarthra trigla Ehr.....	Ro	Triarthra longiseta Ehr. = Filina	
Pompholyx complanta Gosse.....	Ro	longiseta (Ehr.).....	Ro
Scapholeberis mucronata (O.F.M.)...	Cl	Trichotria (Dincharis) tetractis	
Scenedesmus quadricauda (Turp.)		(Ehr.) Harring.....	Ro
Bréb.....	Al	Trochosphaera aequatorialis Semper..	Ro
Simocephalus exspinosus (Koch)....	Cl	Volvox globator Leeuwenhoek.....	Pr

TABLE 1.—ABUNDANCE OF PREDOMINANT ORGANISMS IN PLANKTON OF LARGE RIVERS
(Thousands per cubic meter)

Species	Rock River Sterling, Ill. Summer, 1926	Fox River Altonquin, Ill. Summer, 1916	Wabash River Mt. Carmel, Ill. April, 1927	Mississippi River St. Louis to Cairo June, 1910	Mississippi River Keokuk to St. Louis June, 1910	Ohio River Paducah to Cairo June, 1910
<i>Trachlomonas volvocina</i>	150.0	2.0	1.5	10.3
<i>Difflugia lobostoma</i>	4.1	1.7	1.2	22.4	2.9
<i>Codonella cratera</i>	144.4	8.8	1.2	.6	15.7
<i>Bosmina longirostris</i>	47.6	440.0	8.9
<i>Keratella cochlearis</i>	15.3	3	+	5	6.6	1
<i>Brachionus calyciflorus</i>	91.1	35.2	.9	.1	2
<i>Polyarthra trigla</i>	23.5	5	.6
<i>Synchaeta stylata</i>	1.7	2
<i>Synchaeta pectinata</i>	1.5	26.4	7
<i>Cyclops viridis</i>	181.7	150.0	.1	.5	42.4	3.1
<i>Pediasium duplex</i>3	1.0
<i>Closterium acerosum</i>
<i>Synura uvela</i>	45.41	37.1
<i>Asterionella gracillima</i>	1,293.5	3,520.0	96.0	5.1	4,311.2	3.5
<i>Lysigonium granulatum</i>	18.0
<i>Chydorus sphaericus</i>
<i>Keratella quadrata</i>
<i>Brachionus capsuliflorus</i>	2.4	.4	.6
<i>Eudorina elegans</i>	4.4
<i>Cyclops bicuspidatus</i>	112.9	41.0	.2	2
<i>Scenedesmus quadricauda</i>1	2.0	1
<i>Euglena viridis</i>	4.3
<i>Phacus longicauda</i>	1.0	.8
<i>Tintinnidium fluviatilis</i>	30.3	3.0
<i>Asplanchna brightwellii</i>	1.9	6.6	.9
<i>Filinia longiseta</i>	2.1	2.0	.6	.2	3
<i>Euglena oxyuris</i>	7.4
<i>Euglena acus</i>	1.7	5
<i>Diaphanosoma brachyurum</i>	36.1	8.5
<i>Ceratiium hirundinella</i>	2
<i>Daphnia longispina</i>	3.6	2.5	1.8	2
<i>Brachionus angularis</i>	2.0
<i>Pedalia mira</i>	86.2	4.0
<i>Brachionus budapestinensis</i>	4.8
<i>Moira micrura</i>
<i>Brachionus havanensis</i>3
<i>Conochiloides natans</i>
<i>Leptodora kindtii</i>	26.2	264.0
<i>Microcystis aeruginosa</i>	239.8	880.0
<i>Aphanocapsa</i> sp.	104.2	600.0
<i>Anabaena circinalis</i>

+ = less than 100 per cubic meter.

TABLE 2.—MONTHLY ABUNDANCE OF PLANKTON PREDOMINANTS IN THE ILLINOIS RIVER AT HAVANA, 1896
(Thousands per cubic meter)

Species	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
<i>Lysionium granulatum</i>	124.0	2	96.0	531.0	3,221.0	5,500.0	4,008.0	2,820.0	463.0	657.0	136.0	5.0
<i>Polyarthra trigida</i>	5.6	3.8	28.7	120.7	18.8	20.0	41.5	26.7	3.7	2.0	4.8	21.0
<i>Brachionus calyciflorus</i>	4.0	295.1	6.4	9	2.8	12.2	7.0	4	5	7.6
<i>Codoneia tripartita</i>	1.5	1.0	..	198.5	23.6	50.8	2.2	19.1	23.1	63.2	2.0	1.1
<i>Cyclops bicuspidatus</i>	1.5	10.2	5.7	4
<i>Diaptomus lobosus</i>	3.1	3.6	67.0	13.0	1.5	4.9	3.0	1	8.0	..
<i>Diaptomus lobosus</i>	3.2	4.6	12.2	13.6	3.0	3.1	3.6	9.6
<i>Keratella cochlearis</i>	16.3	33.8	36.2	8.3	4.7	3.7	1.2	6.8	..
<i>Microcystis aeruginosa</i>	3,000.0	4,200.0	2,200.0	1,600.0	1,550.0	8,080.0	1,560.0	28,000.0	19,500.0	12,000.0	8,000.0	2.2
<i>Stentor avella</i>	54.0	73.0	..	124.0	..	2.0	53.6	60.2	299.5
<i>Stentor coeruleus</i>
<i>Notolca striata</i>	3.2	9
<i>Asterionella gracillima</i>	1.6	14,773.0	2,324.0	1.4	1.7
<i>Synchaeta stylata</i>	3.6	3.5	113.1	36.5
<i>Keratella quadrata</i>	1.2	2.2	3.8
<i>Synchaeta pectinata</i>	1.3	7.4	9.2	11.5	3.6	4	20.7	17.6	4
<i>Cyclops bicuspidatus</i>
<i>Brachionus pectinatus</i>
<i>Eudorina elegans</i>	2.3	11.9	4.3	1.7	9.7	3.8
<i>Trachelomonas volvocina</i>	2.2	6.5	2.0	2.0
<i>Pediasium duplex</i>	3.7	10.8	11.5	21.6	26.0	3.6
<i>Bosmina longirostris</i>	15.5	31.0	34.0	12.0	5.7	1.6
<i>Cyclops viridis</i>	3.0	10.8	6.1	1.5	4.5	2.4
<i>Closterium acerosum</i>	3.0	1.5	2.1
<i>Phacus longicauda</i>	2.0
<i>Tintinnidium fluviatilis</i>	1.1	..	2.6	2.9
<i>Filinia longiseta</i>	1.1	..	2.6	1.5	1.3
<i>Asplanchna brightwellii</i>	1.7	..	1.2	3.2	112.0
<i>Euglena oxyuris</i>
<i>Euglena acus</i>
<i>Scenedesmus quadricauda</i>
<i>Ceratiium birundinella</i>
<i>Daphnia longispina</i>
<i>Brachionus angularis</i>
<i>Pedalia mira</i>
<i>Brachionus budapestinensis</i>
<i>Brachionus havanaensis</i>
<i>Conochiloides natans</i>
<i>Diaptomus siciloides</i>
<i>Diaptomus pallidus</i>
<i>Moira micrura</i>

+ = less than 100 per cubic meter.

TABLE 3.—MONTHLY ABUNDANCE OF ORGANISMS TAKEN IN PLANKTON COLLECTIONS FROM SANGAMON RIVER AT MAHOMET, 1928
(Thousands per cubic meter)

Species	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Diatoms, unidentified*	1,400.0	15,600.0	16,665.0	15,000.0	2,666.4	3,333.0	16,665.0	5,590.0	14,000.0	140.0
Navicula spp.*	175.0	2,600.0	1,111.0	2,000.0	266.6	333.3	11,110.0	828.5	1,200.0	2.0
Lysigonium varians*	3	88.0	25,000.0	13.3	235.0	559.0
Centropyxis aculeata*	78.3	23,333.0	6,000.0	666.6	.1	5.6	100.0	115.0
Synedra ulna*	22.2	11.1
Sphinctocystis elliptica*	44.4
Strombidium sp.*	40.0
Coleps hirtus*	20.0
Chilodon cucullus*	20.0
Paramoecium bursaria*	50.0
Cyclops viridis	133.3	6,666.6	2,222.0	918.0	400.0	1.7
Gyrosigma acuminatum*	133.3	16.6	22.2	15.0
Sphinctocystis fibrilis*	13.3	15.5	222.2
Surirella robusta*	13.3	.2
Euglena viridis	4.84	5.0
Euglena oxyuris	3.0	111.1
Oscillatoria spp.*2
Closterium moniliferum
Arcella vulgaris7	27.9
Diffugia acuminata	22.2	222.2
Nitzschia sigmoidea	11.1
Sphinctocystis elliptica*	4.4
Phacus longicauda5
Cyclops serrulatus
Average Temperature, °C.	9.0	15.0	21.0	23.5	25.0	27.5	22.0	20.0	8.3	3.0
Average pH	7.6	7.6	7.6	7.6	7.6	7.6	7.6	7.6	7.6	7.6

*Decanted collections. + = less than 100 per cubic meter.

TABLE 4.—MONTHLY ABUNDANCE OF PLANKTON PREDOMINANTS IN LAKE DECATUR AT LOST BRIDGE, 1923-1924
(Thousands per cubic meter)

Species	June, 1923	July, 1923	Sept., 1923	Oct., 1923	Nov., 1923	Dec., 1923	Feb., 1924	Apr., 1924
<i>Codonella cratera</i>	124.7	1.9	221.2	192.5	562.5	1.0	.1	12.7
<i>Diffugia lobostoma</i>	1.0	15.0	26.1	2.2	+	+	.2	+
<i>Keratella trigla</i>	2.0	6.3	5.1	168.7	.5	+1
<i>Lysigonium cochlearis</i>	136.7	3,625.0	5.0	4,725.0	.1	...	6.2
<i>Pediastrum duplex</i>	27.7	1.7	5.0	2,000.0	123.7	+
<i>Asplanchna brightwellii</i>	2.0	1.1	2.0	5.6
<i>Synchaeta pectinata</i>	1,081.0	2.4	1.1	1	45.0	1.0
<i>Brachionus calyciflorus</i>	21.7	2.5	2.2	3.6	...	2.0
<i>Brachionus capuliflorus</i>	75.4	1.0	4.1	4.5
<i>Cyclops viridis</i>	1,067.2	1.3	1	1.0	12.3
<i>Brachionus angularis</i>	28.3	17.5	30.0	225.0
<i>Eudorina elegans</i>	22,065.1	2.6	1.0	16.8
<i>Pleodorina illinoensis</i>	134.0	3.2	1.2
<i>Scenedesmus quadricauda</i>	27.0	23.7	2.0	5.6
<i>Euglena viridis</i>	2.6	6.8	72.7	225.0
<i>Euglena oxyuris</i>	2.1	2.0	7.2	56.2
<i>Euglena acutissima</i>	2.1	11.7	1.0	11.2
<i>Phacus longicauda</i>	3.5	7.2	10.6	337.5
<i>Filinia longispina</i>	2.0	2.2	2.4
<i>Daphnia longispina</i>	8.7
<i>Pedalia mira</i>	1.2	67.5
<i>Cyclops bicuspidatus</i>	1.2	11.2	.5
<i>Ceratum hirundinella</i>
<i>Diaphanosoma brachyurum</i>	+	1.1

+ = less than 100 per cubic meter.

TABLE 6.—MONTHLY ABUNDANCE OF PLANKTON PREDOMINANTS IN LAKE DECATUR AT LOST BRIDGE, 1927
(Thousands per cubic meter)

Species	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
<i>Diffugia lobostoma</i>1	.1	+	+	+	.1	194.4	85.0	214.3	77.7	30.0	1.0
<i>Codonella cratera</i>	+	+	+	+	34.5	88.8	625.6	387.6	400.0	245.5	199.9	9.0
<i>Polyarthra trigla</i>2	+	+	+	.4	.4	132.0	7.6	288.5	33.0	8.4	+
<i>Keratella cochlearis</i>	+	+	+	+	.1	.1	1.2	12.1	5.4	99.9	.3	+
<i>Bosmina longirostris</i>	+	+	+	+	.2	.1	28.1	1.0	1.17
<i>Cyclops viridis</i>2	+	+	.1	+	+	1.1	.36	.1
<i>Notholca striata</i>	+	+	+
<i>Euglena viridis</i>	33.4	17.7	5.5	115.0	20.0	39.9	25.0
<i>Eudorina elegans</i>	3.3	4.8	20.8	5.0	20.0
<i>Synchaeta stylata</i>	3.1	2.4	25.0	3.5	114.1	7.5
<i>Filinia longisetia</i>4	2.0	3.3	2.9	.1
<i>Brachionus calyciflorus</i>	2.2	2.6	4.2	5.1	.3	15.2
<i>Pediasium duplex</i>3	3.6	1.0	1.0
<i>Lysigonium granulatum</i>	+	20,136.8	11,665.5	20,000.0	4,444.0	8,332.6
<i>Brachionus angularis</i>	200.0	8.8	4.4	3.4
<i>Daphnia longispina</i>	3.1	4.4	5.7
<i>Closterium acerosum</i>
<i>Limnidium fluviatilis</i> *.....3	76.3	83.3	200.0	237.7	65.0
<i>Euglena oxyuris</i>	16.0	115.0	20.0	29.9	52.0
<i>Euglena acus</i>	17.0	5.0	8.5
<i>Brachelomonas volvocina</i> *.....	9,443.5	16,665.0	400.0	1,999.8	444.4
<i>Ceratium hirundinella</i>	7.1	1.2	144.0	3.7
<i>Phacus longicauda</i>	2.3	41.3
<i>Scenedesmus quadricauda</i> *.....	63.8	66.6	400.0	22.2	66.6
<i>Asplanchna brigittewellii</i>	7.5	5.0	7.3
<i>Brachionus budapestinensis</i>	15.0	10.0	3.9
<i>Brachionus havanaensis</i>7
<i>Diaplanosoma brachyurum</i>85
<i>Pedalia mira</i>	2.5	33.1	10.0
<i>Lepidodora kindtii</i>1
<i>Synura uveula</i>	1.2
Average temperature, ° C.....	1.0	3.0	7.5	9.0	20.0	21.0	26.0	28.0	27.0	17.0	11.0	5.0
Average pH.....	7.2	7.2	7.5	7.6	7.6	7.6	7.6	7.8	7.4	7.6	7.4	7.4

* Filter paper or decanted collections. + = less than 100 per cubic meter.

TABLE 7.—MONTHLY ABUNDANCE OF PLANKTON PREDOMINANTS IN LAKE DECATUR AT LOST BRIDGE, 1928
(Thousands per cubic meter)

Species	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
<i>Lyngonium granulatum</i> *	55.5	116.6	...	150.0	9,566.8	203,873.5	43,882.6	9,999.0	6,072.5	14,252.6	22,886.6	77.7
<i>Codonella cratera</i> *	130.0	394.4	526.2	1,099.8	1,387.6	988.7	1,391.5	459.1	803.8	7.6
<i>Diffugia lobostoma</i> *	6.2	+	+	1.1	1.2	15.2	7.7	188.2	794.3	90.5	8.2	5.2
<i>Polyarthra trigla</i> ...	+	+	+	+	2.0	7.3	28.2	12.6	1.3	1	9.5	+
<i>Keratella cochlearis</i> ...	1	+	+	6.5	2.0	22.6	6.6	12.5	18.6	3.0	5.9	+
<i>Synura uvella</i> ...	+	+	+	5.8	2.7	11.1	2.6
<i>Pediastrum duplex</i> ...	+	1.0	8.7	2.5	8	5.1	28.9	2
<i>Keratella quadrata</i>	6.6	10.0	1,727.6	344.4	4,360.0	1,241.5	163.8	11.0	21.1	...
<i>Euglena viridis</i>	1.2	2.5	1.0	10.8	27.0	1
<i>Synchaeta pectinata</i>	+	3.6	18.1	13.8	1.6	2.0	4.0	+
<i>Cyclops viridis</i>	+
<i>Closterium acerosum</i>	3.3	13.6	4.6
<i>Eudorina elegans</i>	1,107.0	43.0	9	8.2	...
<i>Scenedesmus quadricauda</i> *	4.1	...	3.6	28.3	244.4	...	11.1	...
<i>Phacus longicauda</i>	1	...	31.3	31.6	18.8	1.5	...	1.1	8.9	+
<i>Cyclops bicuspidatus</i> ...	1.3	62.5	2.1	9.1	3.5	...
<i>Synchaeta stylata</i>	6.6	262.0	10.0	1.1	...	1.1	...	4.5	+
<i>Brachionus calyciflorus</i>	3.0	3.2	1.1	4.2	1.5	2.2
<i>Brachionus angularis</i>	12.8	9	2.9
<i>Diaphanosoma brachyurum</i>	75.6	799.9	463.8	57.2	1.6	...
<i>Ceriatum hirundinella</i> *	1.5	5.0	13.2	4.6	1.7	...	+
<i>Filinia longseta</i>	2.6	3.6	40.4	37.2	36.3	5.3	...
<i>Diaptomus sicloides</i>	4.5	1.0	2.2	4	2.4	3.3	1.3	...
<i>Asplanchna brigatwellii</i>	1.1
<i>Bosmina longirostris</i>
<i>Euglena oxyuris</i> *	30.0	6.1	2.9
<i>Tintinnidium fluviatilis</i> *	56.5	42.7	3,269.8	10.0	24.4	32.5	858.5	...
<i>Pedalia mira</i>	1.1	11.3	4.3	3.8
<i>Trachelomonas volvocina</i> *	3,305.2	37,356.3	15,697.8	9,946.5	1,216.0	2,222.0	...
<i>Brachionus havanensis</i>
<i>Leptodora kindtii</i>
<i>Conochiloides natans</i>
<i>Anabaena circinalis</i>
<i>Aphanocapsa</i> sp.
Average temperature, °C.	1.0	4.0	7.4	9.5	21.0	22.5	26.6	28.5	14.0	13.0	5.0	22.2
Average pH	7.4	7.6	7.6	7.6	7.6	7.6	7.6	7.6	7.5	7.6	7.6	7.6

*Decanted collections. + = less than 100 per cubic meter.

TABLE 8.—MONTHLY ABUNDANCE OF PLANKTON PREDOMINANTS IN SANGAMON RIVER AT MONTICELLO, 1927
(Thousands per cubic meter)

Species	Mar.	Apr.	May	June	July	Aug.	Nov.
Diatoms, unidentified	1.7	.5	1.0	6.8	.3	1.5	12.0
Synedra ulna	5.1	.5	.2	1.0	36.0
Diffugia lobostoma	.1	+	.4	4.0	3.0	4.0	...
Keratella cochlearis	.14	.1	.3	...
Euglena viridis	14.0	2.5
Ceratium hirundinella	.12
Bosmina longirostris	+7	5.0	...
Notholca striata	+5
Centropages aculeata4	.2
Navicula1
Daphnia longispina8	.1	.1	...
Cyclops bicuspidatus	4.0	.1	4.5	24.0
Pedastrium duplex	3.0	.3	1.5	...
Phacus pleuronectes2	...	3.0	...
Codonella cratera1
Polyarthra trigla1	1.5	...
Brachionus havanaensis3
Brachionus angularis7
Chydorus sphaericus	3.0	...
Scenedesmus quadricauda2	.1
Average temperature, ° C.	9.0	10.0	20.0	22.0	27.0	25.0	8.0
Average pH	7.6	7.6	7.8	7.6	7.8	7.8	7.6
Average gage readings in feet	8.5	10.9	9.3	8.5	5.4	3.8	6.6

+ = less than 100 per cubic meter.

TABLE 9.—MONTHLY ABUNDANCE OF PLANKTON PREDOMINANTS IN SANGAMON RIVER AT MONTICELLO, 1928
(Thousands per cubic meter)

Species	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Diatoms, unidentified†	220.0	429.0	360.0	400.0	14,000.0	1,080.0	330.0	1,082.0	2,300.0	165.0	6,000.0	750.0
Navicula spp.*	45.0	.1	176.0	340.0	641.0	442.9	110.0	507.0	115.0	.3	2,000.0	250.0
Synedra ulna*	22.0	286.0	528.0	1,000.0	11,000.0	572.0	220.0	50.0	12.0	8.2	15.0	150.0
Difflugia lobostoma*	11.0	1.5	1.0	.1	12.0	335.0	22.7	10.0	22.0
Centropages aculeata*	4.5	1.0	9.0	.6	1.0	1.5	1.0	12.0
Difflugia acuminata*	2.02	11.0	1.0	1.01
Polyarthra trigla.	1.0	.31
Filinia longiseta3	1.0	1.0
Notholca striata1	.6
Camptocercus rectirostris3
Cyclops viridis6
Euglena viridis*31
Keratella cochlearis	170.0	37.0	.2	101.0	231.0	165.0	.6
Trachelomonas volvocina	1.0	1.0	2.0	.2
Phacus acuminata*	7.5	24.0	281.0	23,100.0	5.5
Phacus acerosus*	2.02	12.0
Closterium acerosum*	6.0	.325
Euglena oxyuris
Brachionus calyciflorus	2.5
Brachionus angularis611
Brachionus havanaensis6
Codonella cratera*	7.0	3.0
Asplanchna brightwellii	1.01
Daphnia longispina	1.254
Bosmina longirostris	1.1	.4	.1
Cyclops bicuspidatus2	.1	1.5
Cyclops serrulatus116
Synchaeta pectinata
Keratella quadrata
Scenedesmus quadricauda*	20.0	22.0
Arcella vulgaris*	2.5	20.0
Brachionus capsuliflorus11
Phacus pleuronectes*	2.0	12.0	5.5
Average temperature, ° C.	4.0	2.0	6.5	13.0	17.0	22.0	24.0	26.0	23.0	20.0	8.0	5.0
Average pH	7.4	7.6	7.6	7.6	7.6	7.6	7.6	7.6	7.6	7.6	7.6	7.6
Average gage readings	8.3	8.7	6.0	6.9	4.6	4.7	4.9	2.4	2.4	3.5	4.4	6.0

*Decanted collections. †Mostly bottom forms. + = less than 100 per cubic meter.

TABLE 10.—MONTHLY ABUNDANCE OF PLANKTON PREDOMINANTS IN PARK POND AT DECATUR, 1927¹
(Thousands per cubic meter)

Species	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
<i>Diaptomus pallidus</i>	6.0	13.0	30.0	300.0	10.0	7.8	1.8	.4	.2	296.0	30.0
<i>Bosmina longirostris</i>1	.5	1.0	4.0	.5	125.0	5.8	.2	.1	29.6	2.0
<i>Daphnia longispina</i>	2.0	1.0	4.0	40.0	275.0	20.0	18.5	66.0	64.0	37.0	50.0
<i>Codonella cratera</i>8	1.0	4.0	.6	600.0	382.0	270.0	6.6	400.0	1,480.0	2.0
<i>Keratella cochlearis</i>	1.2	14.0	34.0	350.0	530.0	216.0	49.0	44.0	108.0	74.0	46.0
<i>Polyarthra trigla</i>	2.0	8.0	60.0	170.0	22.0	3.0	101.0	13.2	12.0	11.1	.2
<i>Cyclops viridis</i>	1.0	44.0	200.0	40.0	35.0	235.0	99.5	8.8	16.0	7.9	.6
<i>Diflugia lobostoma</i>1	+	8.0	200.0	285.0	125.0	92.5	66.0	480.0	37.0	24.0
<i>Euglena viridis</i>4	1.04	5.0	35.5	10.0	.1	.21
<i>Phacus longicauda</i>8	4.0	.6	1.0	5.0	.5	1.1	.4	3.21
<i>Chydorus sphaericus</i>2	.2	2.0	.24	.8	150.0	1.0
<i>Cyclops bicuspidatus</i>	1.0	5.0	10.0	30.0	5.03	3.0
<i>Conochiloides natans</i>	2.0	8.0	6.0	2.0	8.0
<i>Filinia longiseta</i>2	3.0	1.2	2.0
<i>Closterium acerosum</i>	6.0	1.02	1.8	2.4
<i>Keratella quadrita</i>2	.2	4.0	1.01
<i>Brachionus calyciflorus</i>2	.4	.4	25.0	8.2	.12
<i>Synchaeta pectinata</i>	150.0	4.0
<i>Brachionus havanaensis</i>2	.1	170.0	202.5	79.5	37.4	1.6
<i>Asplanchna brightwellii</i>	4.0	15.0	7.2	1.0	3.3
<i>Trachelomonas volvocina</i>	8.0	185.0	125.0	88.0	32.0	222.0	.8
<i>Brachionus angularis</i>	1.3	3.7	9.0	13.2	4.0	1.8	.1
<i>Microcystis aeruginosa</i>	1,000.0	52.0	.5	.4
<i>Ceratium hirundinella</i>	624.5	3.08	4.0
<i>Diaphanosoma brachyurum</i>	4.4 ^a	.2	2.2
<i>Pediastrum duplex</i>	6.4 ^a	13.5	13.2	4.0	11.1	.2
<i>Scenedesmus quadricauda</i>7	2.2	1.0
Average temperature, ° C.....	3.5	10.0	12.0	18.5	23.0	25.0	28.0	22.5	18.0	12.0	5.0
Average pH.....	6.6	6.6	7.0	7.2	7.6	7.0	6.6	7.0	7.2	6.6	6.6

¹Similar collections made in 1926 and 1928 contained the same species, except that *Pediastrum duplex* and *Scenedesmus quadricauda* were not taken in 1926, and *Placus longicauda*, *Chydorus sphaericus*, *Cyclops bicuspidatus*, and *Brachionus angularis* were not taken in 1928. One additional species, *Brachionus calyciflorus*, appeared in 1928.

TABLE 11.—MONTHLY ABUNDANCE OF PLANKTON PREDOMINANTS IN PARK POND AT URBANA, 1928¹
(Thousands per cubic meter)

Species	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
<i>Scenedesmus quadricauda</i> *	1,200.0	11.0	1,700.0	1,200.0	13,332.0	140,000.0	13,330.0	352.0	7,777.0	2,055.3	755.4
<i>Trachomonas volvocina</i> *	1,440.0	1.1	6,000.0	3,000.0	166.6	24,200.0	8,888.0	12,000.0	6,666.0	8,221.4	1,888.7
<i>Codonella cratera</i> *	1,200.0	2,222.0	119.0	1,200.0	33.1	3,300.0	711.0	1,000.0	2,222.0	4,110.7	1,885.8
<i>Polyarthra trigla</i> *	1,330.0	200.0	170.0	6.0	34.2	55.0	93.0	35.2	22.5	60.0	3.1
<i>Bosmina longirostris</i> ...	15.2	8.0	15.2	2,250.0	133.0	176.4	108.5	26.4	150.0	9.0	20.8
<i>Asplanchna brightwelli</i> ...	5.7	1.2	54.4	.7	1.9	2.0	6.2	17.6	1.0	6.0	15.6
<i>Keratella cochlearis</i> ...	1.0	10.0	.6	.8	1.0	8.4	620.0	186.0	13.7	135.0	260.0
<i>Daphnia longispina</i>1	2.3	7.0	1.0	57.0	54.0	.387.5	.220.0	11.5	6.0	2.0
<i>Cyclops virens</i> ...	15.2	8.0	30.0	28.0	10.0	252.0	124.0	.110.0	1.2	.60.0	20.8
<i>Cyclops bicuspidatus</i>1	.2	1.7	17.8	15.2	12.6	.110.0	.110.0	.11.5	.60.0	5.2
<i>Lysigonium calyciflorum</i> ...	60.0	.1	40.0	90.0	5,832.7	540.0	.110.0	.110.0	.11.5	.60.0	20.8
<i>Pediastrum duplex</i> *	.1	.2	13.6	.1	1,666.5	900.0	.110.0	.110.0	.11.5	.60.0	20.8
<i>Dinifugia lobostoma</i> *	.1	.2	13.6	.1	1,666.5	900.0	.110.0	.110.0	.11.5	.60.0	20.8
<i>Euglena viridis</i>1	.2	13.6	.1	1,666.5	900.0	.110.0	.110.0	.11.5	.60.0	20.8
<i>Brachionus angularis</i>1	.2	13.6	.1	1,666.5	900.0	.110.0	.110.0	.11.5	.60.0	20.8
<i>Phacus longicauda</i> *	.1	.2	13.6	.1	1,666.5	900.0	.110.0	.110.0	.11.5	.60.0	20.8
<i>Tintinnidium fluviatilis</i> *	.1	.2	13.6	.1	1,666.5	900.0	.110.0	.110.0	.11.5	.60.0	20.8
<i>Conochiloides natans</i>1	.2	13.6	.1	1,666.5	900.0	.110.0	.110.0	.11.5	.60.0	20.8
<i>Aplanocapsa</i> sp.1	.2	13.6	.1	1,666.5	900.0	.110.0	.110.0	.11.5	.60.0	20.8
<i>Brachionus lavanaensis</i>1	.2	13.6	.1	1,666.5	900.0	.110.0	.110.0	.11.5	.60.0	20.8
Average temperature, ° C.	20.0	6.0	10.0	18.0	22.0	25.0	26.5	16.0	11.0	6.0	3.0
Average pH	7.6	7.4	7.4	7.6	7.6	7.8	7.8	7.6	7.6	7.6	7.6

*Decanted collections. ¹Similar collections made in 1927 contained the same species except that *Brachionus calyciflorus*, *Euglena viridis*, *Phacus longicauda*, *Conochiloides natans*, *Aplanocapsa* sp., and *Brachionus lavanaensis* were not taken in 1927. Two species, *Keratella quadrata* and *Chydorus sphaericus*, were taken in 1927 but not in 1928.

TABLE 12.—MONTHLY ABUNDANCE OF PLANKTON PREDOMINANTS IN OX-BOW POND NORTH OF URBANA, 1928
(Thousands per cubic meter)

Species	Feb.	Mar.	Apr.	May	June	July	Aug.
<i>Navicula</i> spp.*	175.0	280.0	4,400.0	1,266.5	100.0	300.0	17,800.0
<i>Dinifugia lobostoma</i>	12.0	4.0	70.0	17.5	7.2	143.0	50.0
<i>Chydorus sphaericus</i>4	6.0	28.0	7.0	14.4	6.6
<i>Campocercus rectirostris</i>2	.1	5.2	.3
<i>Feridinium tabulatum</i>	2	15.0	17.5
<i>Synura uvela</i> *.....	10.0	8.0
<i>Synura</i>	3.0	4.0
<i>Notolca striata</i>	4.0	3.0
<i>Simocephalus vetulus</i>	1.8	.3
<i>Cyclops serrulatus</i>	7.0	.7
<i>Cyclops bicuspidatus</i>	1.0	.5	1.8	3.3
<i>Cyclops viridis</i>	17.5	35.0	6.0	28.6	300.0
<i>Arcella vulgaris</i>	1.0	9.0	8.8
<i>Trachelomonas hispida</i> *.....	7.7	1.0	7.2	6.6
<i>Euglena viridis</i>	17.8	126.6	5.4
<i>Phacus longicauda</i>	8.9	1.0	100.0	200.0	25,000.0
<i>Centropomys aculeata</i>	1.4	.3	.1
<i>Daphnia longispina</i>3	.3
<i>Lepadella acuminata</i>	1.01	4.4
<i>Closterium acerosum</i>
<i>Dinifugia acuminata</i>	1.4	20.0
<i>Cryptomonas ovata</i> *.....	3.5	.1	335.0	4.0
<i>Daphnia pulex</i>	2,532.5	1,200.0
<i>Keratella cochlearis</i>1	21.6
<i>Trachelomonas volvocina</i> *.....
<i>Polyarthra triga</i>	3	660.6	880.0
<i>Sapphiteberis mucronata</i>	12.0
<i>Platylas quadricornis</i>	54.1	35.2	9.9
<i>Pleuroxus denticulatus</i>1	2.2
<i>Phacus denticulatus</i>3
<i>Brachionus pectinatus</i>	66.6	45.0
<i>Brachionus patulus</i>	4.4	2.0
<i>Euglena spirogyra</i>	2.0	190.9	666.6	440.0
<i>Eudaima elegans</i>	178.0
<i>Brachionus havanaensis</i>	800.0
Average temperature, ° C.....	3.0	7.0	14.0	18.0	20.0	25.0	28.0
Average pH.....	7.4	7.5	7.6	7.6	7.6	7.6	7.6

*Decanted collections.

TABLE 13.—MONTHLY ABUNDANCE OF PLANKTON PREDOMINANTS IN TEMPORARY POND WEST OF SEYMOUR, 1928
(Thousands per cubic meter)

Species	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.
<i>Cyclops bicuspidatus</i>	2.2	12.0	99.0	23.0	3.0	.2
<i>Camptocercus rectigaris</i>	1.5	.4	13.2	6.3	4.0	6.0	56.0
Diatoms, unidentified*.....	6,600.0	12,500.0	8,000.0	5,000.0	1,980.0	53,400.0	18,750.0
<i>Trachelomonas volvocina</i> *.....	110.0	1,000.0	2,400.0	20,000.0	26,000.0	3,560.0	1,500.0
<i>Scenedesmus quadricauda</i> *.....	11.0	50.0	160.0	25.0	20.0	18.0
<i>Centropages aculeata</i>	1.5	8.0	1.3	12.0	.4	1.2	37.0
<i>Diifugia lobostoma</i> *.....	220.0	25.0	4.0	20.0	30.0	71.0
<i>Diifugia acuminata</i>3	4.0	.3	.5	.2	.4
<i>Placus pleuronectes</i>	11.0	100.0	80.0	1,000.0	20,000.0	890.0
<i>Nodiola striata</i>	1.5	8.0	.6	1.2
<i>Synura uveilla</i>	110.0	50.0	5,320.0
<i>Pantocampus</i> sp.....	.4	1.22	1.2
<i>Peridinium tabulatum</i> *.....	1,100.0	1,500.0	24,000.0	100.0	1,125.0
<i>Trachelomonas hispida</i> *.....	10.0	100.0	320.0	3,000.0	13,300.0	26,700.0	750.0
<i>Simoccephalus vetulus</i>3	54.0	4.0
<i>Rosmina longirostris</i>3	1.8	2.0
<i>Eubranclipus</i> sp.....1	.1
<i>Arcella vulgaris</i>3	.5
<i>Lecane unguatata</i>	2.0	.2	6.0
<i>Lepadella acuminata</i>	30.0	20.025
<i>Euglena viridis</i>	160.0	100.0	53,200.0	71,800.0
<i>Euglena spirroides</i> *.....	8.0	266.0	534.0
<i>Alona affinis</i>2	1.8	1.0
<i>Testudinella patina</i>2	.2	5.6
<i>Chydorus sphaericus</i>2
Average temperature, ° C.....	3.0	1.0	10.0	18.0	20.0	26.0	Dry	Dry	8.0
Average pH.....	7.6	7.6	7.6	7.6	7.6	7.6	7.4

*Decanted collections.

TABLE 14.—ABUNDANCE OF PLANKTON PREDOMINANTS IN BEACH PONDS ON SHORE OF LAKE MICHIGAN NEAR GARY, INDIANA
Obtained from averages of collections made in May, 1927, 1928, and 1929
(Thousands per cubic meter)

Species	Pond 1	Pond 5	Pond 14	Pond 60	Pond 93	Pond 94	Pond 95	Pond 96
Diatoms, unidentified.....	82.0	260.0	5,961.3	304.0	24,000.0	240.0	567.5	1,600.0
Arella vulgaris.....	.3	7.6	15.7	2.0	2.4	1.2	19.5	1.6
Peridinium tabulatum.....	150.0	236.6	26.1	.2	3.0	.4	27.3	80.0
Monostyla lunaris.....	.4	.8	.4	.4	.6	.2	.4	.4
Daphnia pulex.....	.3	.3	.4	.8	1.2	7.2	2.1	3.2
Cyclops viridis.....	3.0	.3	21.0	12.0	12.0	2.4	15.0	12.0
Ostracods, unidentified.....	4.7	.8	39.0	6.0	12.0	.6	26.5	16.0
Chydorus sphaericus.....	1.5	1.3	17.4	.2	6.0	5.9
Lecanoreus epistomum.....	6.0	2.2	3.673
Ceriodaphnia sp.....	.1	2.1	3.9	.4	1.24
Ceratum hirundinella.....	1.4	.2
Testudinella patina.....	1.1	.2
Daphonius sanguineus.....	1.1	20.0	.2	3.0	.2	2.7	.4
Cyclops bicuspidatus.....	4.7	3.9	.4	36.0	.4	6.0	8.0
Cyclops serrulatus.....	2.6	1.3	2.1	2.0
Daphnia longispina.....4	1.4	.4	2.4	14.4
Canthocamptus sp.....1	1.0	.2	4.0
Trichotria tetractis.....2	1.3	1.2	.1	.8
Bosmina longirostris.....	5.0
Diaphanosoma.....	7.0	7.6
Diaphanosoma seriale.....	260.0	120.6	36.0	143.5
Diffugia pyramidalis.....1	4.04
Lepadella acuminata.....2	3.02
Cladocera, nonidentified.....2	.1	.2
Fragilaria crotonensis*.....	2,000.0	3,600.0	4.0
Staurastrum spp.....	5	39.6
Cosmarium spp.....	6.0	33.0
Crucigenia spp.....4	3.6
Chroococcus.....2	1.3
Eudorina elegans.....1	1.2
Pleuroxus denticulatus.....31	2.0
Acroporus bairpae.....1	3.6
Synura uella.....1
Placus acuminata.....1
Polarthra trigla.....	11.36
Keratella cochlearis*.....	4.0
Volvox globator.....	6.0
Centropyxis aculeata.....	7.24
Filinia longiseta.....1
Simocephalus eximiosus.....41
Simocephalus vetulus.....2
Keratella quadrata.....6
Scapholeberis mucronata.....	1.2

*Abundant in Lake Michigan.

TABLE 15.—AVERAGE SUMMER ABUNDANCE OF PLANKTON ORGANISMS IN FLOOD PLAIN LAKES, JUNE, JULY, AUGUST
(Thousands per cubic meter)

Species	Rock River Slough, So. of Erie, Ill. 1926	Hatwood Slough, Erie, Ill. 1926	Slough near Byron, Ill. 1926	Slough near Grand Detour, Ill. 1926	Slough near Colona, Ill. 1926	Horseshoe Lake, Ill. 1928	Wolf Lake, Union Co., Ill. 1928	Macon Lake, Inverness, Miss. 1927	Lake Dawson, Inverness, Miss. 1927
<i>Trachelomonas volvocina</i>	9.9	10.0	32.0	36.0	4.8	81.0	30.0	4.0	16.0
<i>Diffugia lobostoma</i>	424.5	4	32.0	100.0	8.6	5	9.0	2	9.6
<i>Codonella cratera</i>	76.5	454.9	32.0	12.6	17.7	2	50.0	3.4	1.1
<i>Bosmina longirostris</i>	1.5	61.0	2.0	10.4	17.4	1.5	18.2	4.0	1.6
<i>Keratella cochlearis</i>	330.0	67.3	1.0	70.0	134.4	5.4	1.2	2.0	3.2
<i>Brachionus calyciflorus</i>	9.9	4.0	128.0	127.7	9.0	2.5	1.2	4	16.0
<i>Synchaeta</i> spp.....	8.1	100.2	3.0	5.0	15.6	2	1.3	4	16.0
<i>Pedastum duplex</i>	53.3	32.0	.4	.6	3	.2	4
<i>Closterium acerosum</i>	20,000.0	1,880.0	1.6	300.0	4	24.0
<i>Lysigonium granitum</i>	1.2	544.0	1	4	5	1
<i>Brachionus spiculiferus</i>	10.3	32.0	12.8	177.2	54.0	7.0	40.0	1
<i>Eudonia elegans</i>	84.3	331.6	83.2	5.4
<i>Cyclops bicus</i>	89.1	46.2	5.2	27.0	1.0	1.8	4
<i>Scaphosoma quadricauda</i>	6.6	36.0	96.0	7.8	29.0	1.0	6.0	1.6
<i>Euglena viridis</i>	7.8	75.0	11.0	3.6	1.3	1	4.0	1
<i>Asplanchna balticwellii</i>	9.3	13.0	6.0	2	3	1
<i>Filinia longicauda</i>	4.6	2.6	120.0	13.5	1	2.0	1
<i>Euglena oxyuris</i>	7.8	73.3	800.0	72.0	4.0	42.0	6.0	1
<i>Euglena acus</i>	1.0	32.0	2	12.0	1.6
<i>Diaphanosoma brachyurum</i>	36.3	5.0	35.0	16.2	1.5	2.0	1.6
<i>Daphnia birundinella</i>	6.0	14.0	31.0	108.0	2.0	1	14.0	1
<i>Brachionus angularis</i>	66.0	10.0	480.0	1.0	24.0	16.0	4.8
<i>Pedalia nira</i>	153.8	9.0	3	3
<i>Brachionus budapestinensis</i>	7.2	1.3	222.0	2.0
<i>Moina micrura</i>	13.0	6.0
<i>Moina brachyata</i>	3.1
<i>Brachionus hayanaensis</i>
<i>Conochiloides natans</i>
Area in acres.....	1.2	5.0	1.0	2.0	12.0	1,800.0	500.0	1,000.0	2,000.0
Average depth in feet.....	8.0	4.0	2.0	3.0	3.0	5.0	6.0	6.0	10.0

TABLE 17.—MONTHLY AVERAGES OF VELOCITY AND AGE OF WATER IN THE SANGAMON RIVER, 1928,
CORRELATED WITH THE ABUNDANCE OF PLANKTON
(*abd.* = *abundant*; *com.* = *common*; *occ.* = *occasional*)

Month	Velocity in Feet per Hour	Gage Readings at Monticello in Feet	Age of Water and Relative Abundance of Plankton			
			Maohmet	Monticello	Rhea's Bridge	Lost Bridge
February.....	9,000	8.72	19.9 hr.	1 da., 13.2 hr.	5 da., 13.2 hr. Plankton scarce	10 da., 1.0 hr. Plankton scarce
March.....	2,500	6.08	3 da.	5 da., 3.1 hr.	19 da., 23.5 hr. Plankton occ.	35 da., 17.8 hr. Plankton com.
April.....	2,200	6.94	3 da., 9.6 hr.	5 da., 16.8 hr. Plankton scarce	22 da., 16.9 hr. Plankton occ.	40 da., 21.6 hr. Plankton com.
May.....	1,260	4.60	5 da., 10.5 hr.	11 da., 6.6 hr. Plankton occ.	39 da., 15.4 hr. Plankton com.	71 da., 17.8 hr. Plankton abd.
June.....	2,340	4.72	3 da., 5.1 hr.	5 da., 8.2 hr. Plankton occ.	21 da., 8.3 hr. Plankton com.	38 da., 15.1 hr. Plankton abd.
July.....	1,800	4.92	4 da., 2.7 hr.	7 da., 21.4 hr. Plankton scarce	27 da., 18 hr. Plankton abd.	50 da., 5.2 hr. Plankton abd.
August.....	1,080	2.46	6 da., 22.3 hr.	13 da., 3.6 hr. Plankton occ.	46 da., 6 hr. Plankton abd.	83 da., 16.8 hr. Plankton abd.
September.....	1,500	2.49	5 da.	9 da., 11.3 hr. Plankton occ.	33 da., 9.2 hr. Plankton abd.	62 da., 8.3 hr. Plankton abd.
October.....	720	3.58	10 da., 9.4 hr.	19 da., 17.5 hr. Plankton com.	69 da., 9 hr. Plankton com.	125 da., 13.5 hr. Plankton abd.
November.....	1,720	4.48	4 da., 8.4 hr.	8 da., 6.2 hr. Plankton scarce	29 da., 1 hr. Plankton occ.	52 da., 13.3 hr. Plankton abd.
December.....	3,600	6.00	2 da., 1.8 hr.	3 da., 22.7 hr. Plankton very scarce	13 da., 21 hr. Plankton very scarce	25 da., 2.7 hr. Plankton com.
Equivalent mileage from source.....			34	57	228	409

TABLE 18.—AVERAGE ABUNDANCE OF PREDOMINANT ORGANISMS IN PLANKTON OF THE SANGAMON RIVER, INCLUDING LAKE DECATUR, JULY, 1928, SHOWING CORRELATION WITH AGE OF WATER
(Thousands per cubic meter)

Species	Mahomet	Monticello	Rhea's Bridge	Lost Bridge
Diatoms (mostly bottom forms).....	48,000.0	20,000.0	37.0	.3
Cyclops viridis.....	.5	.5	6.0	3.6
Diiflugia lobostoma.....	33.3	70.0	15.0
Euglena viridis*.....	24.0	180.0	344.4
Trachelomonas volvocina*.....	24.0	3,600.0	3,305.2
Closterium acerosum.....3	.5	.3
Brachionus angularis.....+	.1	3.2
Bosmina longirostris.....4	2.0	.1
Cyclops bicuspidatus.....2	.2	31.6
Scenedesmus quadricauda.....	20.0	32.0	1,107.0
Brachionus capsuliflorus.....+	1.0	No June record
Diaphanosoma brachyurum.....	36.0	12.8
Polyarthra trigla.....+	7.5
Keratella cochlearis.....+	22.6
Moira micrura.....	5.0
Brachionus calyciflorus.....	4.0	10.0
Chydorus sphaericus.....	1.0	1.2
Asplanchna brightwellii.....2	1.0
Lysigonium granulatum*.....6	1.0
Codonella cratera.....	200,000.0
Pediastrum duplex.....	1,000.0
Synchaeta pectinata.....	2.5
Limnoidium fluviatilis.....	10.8
Ceratium hirundinella.....	42.7
Filinia longiseta.....8
Diaptomus siciloides.....	2.6
Phacus longicauda.....3
Pedalia mira.....	1.5
Brachionus havanensis.....5
Lepidodora kindtii.....1
Euglena oxyuris.....3
Age of water in days.....	3	6	20	40

*Decanted collections. + = less than 100 per cubic meter.

TABLE 19.—DEVELOPMENT OF PLANKTON IN LAKE DECATUR, 1923-1928
Averages for June, July, and August Collections
(Thousands per cubic meter)

Species	1923	1926	1927	1928
<i>Pedalia mira</i>	1.0	1.5	2	4.3
<i>Euglena oxyuris</i>	1.3	.5	45.8	2.4
<i>Lysonium granulatum</i>	68.3	891.2	10,667.4	90,214.0
<i>Codonella cratera</i>	63.3	33.4	365.7	1,158.7
<i>Diffugia lobostoma</i>	+	25.7	93.1	70.4
<i>Polyarthra trigla</i>	8.0	6.5	53.3	16.0
<i>Keratella cochlearis</i>	4.1	6.2	6.2	11.9
<i>Pediastrum duplex</i>	14.7	42.1	2.7	2.8
<i>Euglena viridis</i>	13.9	3.8	49.4	1,982.1
<i>Cyclops viridis</i>	533.7	3.9	.3	11.8
<i>Eudorina elegans</i>	11,033.8	6.6	8.6	4.5
<i>Scenedesmus quadricauda</i>	1.6	2.1	43.5	383.6
<i>Phacus longicauda</i>	1.0	.4	.8	10.7
<i>Synchaeta pectinata</i>	541.7	21.2	3.6
<i>Brachionus calyciflorus</i>	13.6	1.6	3.8
<i>Brachionus angularis</i>	14.4	3.0	2.8
<i>Filinia longiseta</i>	4.6	5.7	6.5
<i>Asplanchna brightwellii</i>	1.0	4.1	.5
<i>Brachionus capsuliflorus</i>	38.2	9.8
<i>Daphnia longispina</i>	1.7	2.6
<i>Pleodorina illinoensis</i>	52.0
<i>Closterium acerosum</i>1
<i>Ceratiium hirundinella</i>	180.1	2.7	292.1
<i>Diaphanosoma brachyurum</i>9	1.1	5.5
<i>Bosmina longirostris</i>	5.0	9.7	1
<i>Tintinnidium fluviatilis</i>	1.8	53.2	1,107.4
<i>Trachelomonas volvocina</i>	1.3	18,766.4
<i>Cyclops bicuspidatus</i>	133.7	8,702.8	16.3
<i>Diaptomus siciloides</i>	4.4	15.5
<i>Leptodora kindtii</i>1	15.8
<i>Aphanocapsa</i> sp.....8	+
<i>Microcystis aeruginosa</i>	10.2
<i>Synchaeta stylata</i>	9.3	3.7
<i>Brachionus havanaensis</i>	1.2	.1
<i>Euglena acus</i>	8.3
<i>Brachionus budapestinensis</i>
<i>Conochiloides natans</i>
<i>Anabaena circinalis</i>	400.0

+ = less than 100 per cubic meter.

TABLE 20.—ABUNDANCE OF PLANKTON PREDOMINANTS IN SERIES OF LAKES IN
WAUKESHAW COUNTY, WISCONSIN, SEPTEMBER, 1927
(Thousands per cubic meter)

Species	Oconomowoc Lake	Pewaukee Lake	Lulu Lake
<i>Peridinium</i> spp.	700.0
<i>Glenodinium</i> sp.	85.5
<i>Diufugia globulosa</i>	5.5
<i>Asplanchna sieboldii</i> ..	7.0
<i>Cyclops leuckarti</i> * ..	14.0
<i>Diathela longispina</i> * ..	1.0
<i>Daphnia retrocurva</i> * ..	1.3
<i>Bosmina longispina</i> * ..	1.4
<i>Chydorus sphaericus</i> ..	3	1.0
<i>Cedospheerium naegelianum</i> ..	52.5	2,000.0
<i>Polyarthra hirundinella</i> ..	350.0	500.0	528.0
<i>Keratella cochlearis</i> ..	14.0	35.0	2.0
<i>Diaptomus oregonensis</i> ..	24.5	400.0	594.0
<i>Synedra acus</i> ..	140.7	15.0	825.6
<i>Flagellaria crotonensis</i> ..	15.0	300.0	2,640.0
<i>Scaphesmus quadricauda</i> ..	1,400.9	40.0	198.0
<i>Pedastum duplex</i> ..	7	750.0	137.5
<i>Chirococcus</i> sp.	7.0	1,500.0	26.4
<i>Aphana sphaerula</i> ..	140.0
<i>Microcystis aeruginosa</i>	100.0
<i>Ceriodaphnia lacustris</i>	2.5
<i>Codonella cratera</i>
<i>Euglena viridis</i>
<i>Dinobryon sertularia</i>
<i>Bosmina longirostris</i>	25.0	1,370.0
<i>Asterionella gracillima</i>	3.0	66.0
<i>Lysigonium granulatum</i>	96.0	3,300.0
<i>Cyclops viridis</i>	4,000.0	13,200.0
<i>Pompholyx complanata</i>	3.0
<i>Synchaeta pectinata</i>	52.8
<i>Diaphanosoma brachyurum</i>	66.0
Mean depth in meters.	9.5	3.9	2.0

*Deep lake predominants.

TABLE 21.—ABUNDANCE OF PLANKTON PREDOMINANTS IN REPRESENTATIVE BODIES OF WATER, BASED ON SUMMER AVERAGES (JUNE, JULY, AND AUGUST), SHOWING THE RELATION OF THE DIFFERENT COMMUNITIES
(Thousands per cubic meter)

Species	Stable Stream	Impounded Stream	Young Stream	Perennial Pond	Temporary Pond	Glacial Lake
<i>Microcystis aeruginosa</i>	23,333.0	2.5	95.6	549,812.0
<i>Trachelomonas volvocina</i>	23,256.0	6,872.6	50.8	11,280.1	5,000.0
<i>Polyarthra triida</i>	74.6	24.1	+	164.3	3.0	22.4
<i>Brachionus calyciflorus</i> ¹	166.5	4.7	.4	47.4
<i>Diaphnia globulosa</i> ²	23.5	7.1
<i>Keratella cochlearis</i>	17.5	7.2	.3	284.6	+	87.4
<i>Diaphnia lobostoma</i>	19.9	47.5	12.7	340.4	42.0
<i>Codonella cratera</i>	1,967.0	405.3	1.1	440.6
<i>Cyrdorus sphaericus</i>3	+	5.0	2.7
<i>Lysigonium granulatum</i>	4,303.0	25,480.2	262.0	1,242.6
<i>Scenedesmus quadricauda</i>	37.7	.8	22.2	40.0	2.0
<i>Scenedesmus bicuspidatus</i>	9.6	107.7	+	11,574.1	6.0
<i>Brachionus capsuliflorus</i> ¹	2.8	12.0	1.3
<i>Phacus longicauda</i>	5.7	3.2	503.6	.2
<i>Asterionella gracillima</i>	2.6	139.9
<i>Eudorina elegans</i>	24.4	2,763.5	20.0	1.6
<i>Bosmina longirostris</i>	4.9	3.7	1.0	124.8	4.9
<i>Cyclops viridis</i>	2.0	137.4	.1	197.5	2.0
<i>Pedastrium duplex</i>	65.8	13.6	.5	244.8	2.7
<i>Brachionus angularis</i> ¹	62.8	5.1	82.3
<i>Filinia longiseta</i> ¹	5.8	4.2	10.7
<i>Conochiloides natans</i> ¹	17.2	48.4
<i>Euglena acus</i>	196.9
<i>Euglena viridis</i>	2,145.4	512.3	23.4	2,226.1	10,000.0
<i>Euglena oxyuris</i>	1,821.0	12.5
<i>Diaphanosoma brachyurum</i>	2.6	1.8	5.49
<i>Tintinnidium fluviatilis</i> ¹	1,551.0	290.3	71.8
<i>Pedalia mira</i> ¹	18.1	1.7
<i>Closterium acerosum</i>6
<i>Asplanchna brightwellii</i>	4.3	1.4	.1	2.7	2.0
<i>Brachionus budapestinensis</i>	26.4	2.0	1.7

TABLE 21—(Concluded)

Species	Stable Stream	Impounded Stream	Young Stream	Perennial Pond	Temporary Pond	Glacial Lake
<i>Moina micrura</i> ¹	.7+
<i>Lepidodora kindtii</i>	+
<i>Brachionus calanoides</i>3	73.2
<i>Brachionus calanoides</i>	1.4	118.7	.1	107.8	.8	470.7
<i>Daphnia pulex</i>2	47.3
<i>Daphnia pulex</i>7	80.9	.5	253.0
<i>Daphnia longispina</i>1	1.0	1.4
<i>Daphnia longispina</i>	33.6	5.0
<i>Synchaeta selysi</i>	5.5	141.0
<i>Synchaeta selysi</i>	150.0	3.2
<i>Apicocerca sp.</i>	1,500.0	4.1	62.0	758.7
<i>Artemia salina</i>	100.0	18,132.5
<i>Artemia salina</i>	2.4	6.0
<i>Artemia salina</i>	3.0
<i>Cyclops vernalis</i>	1.0
<i>Camptocercus rectirostris</i> ³	5.0
<i>Simocercus vernalis</i>	5,000.0
<i>Trachelomonas hispida</i>7
<i>Lepadella acuminata</i>	2.5
<i>Lepadella pulex</i>	1.7
<i>Platyias quadricornis</i>	11.0
<i>Scapholeberis mucronata</i>6
<i>Pleuroxus denticulatus</i>	10.0
<i>Brachionus patulus</i>	29.3
<i>Fragilaria crotonensis</i> ²	1.3
<i>Notholca retrocurva</i> ²	1.9
<i>Daphnia retrocurva</i> ²	1.9
<i>Bosmina longispina</i> ²	5.8
<i>Cyclops leuckarti</i> ²	4.9
<i>Diaptomus oregonensis</i> ²	4.9
<i>Diaptomus minutus</i> ²	12.0
<i>Epischura lacustris</i> ²

¹Stable river predominant. ²Glacial Lake predominant. ³Temporary pond predominant. + = less than 100 per cubic meter.

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(See also pages 63-86.)

91

- Facultative planktonts. 8
Filinia longiseta. . . 14, 16, 32, 40, 44, 45, 59
 Finger Lakes. 31
 Fish, C. J. 31, 32
 Food. 56
 Forbes, S. A. 34
 Forel, F. A. 22
 Fox River. 16
Fragilaria crotonensis. 31, 35
 Galtsoff, P. S. 14, 15, 17, 19
 Gary, ponds near. 34
 Great Lakes. 30, 31, 32
 Green Lake. 22, 31, 32
 Green River. 21
 Griffith, B. M. 55
 Harring, H. K., and Myers, F. J. . . . 25, 54
 Heleoplankton. 8
 Hensen, V. 7
 Horseshoe Lake. 25, 39
 Hydrogen-ion concentration. . . 12, 18, 20, 23
 24, 25, 26, 27, 39, 54, 56
 Illinois-Mississippi Canal. 17, 28, 44
 Illinois State Natural History Survey. . 39
 Illinois State Water Survey. 55
 Illinois River. 14, 15, 34, 37, 45, 51, 57
 Incidentals. 10
 Influentals. 9
 Juday, C. 29, 32, 57
 Juday, C., and Wagner, Geo. 56
 Keokuk Dam. 19
 Keokuk Lake. 30
 Keratella. 30
 aculeata. 33
 cochlearis. 14, 15, 16, 18, 31, 34
 35, 36, 39, 44, 57, 59
 quadrata. 16, 31, 32, 40, 44, 57
 Kofoed, C. A. 14, 15, 21, 25, 27, 34, 44
 45, 46, 51, 52, 53, 56
 Kolkwitz, R. 7
 Kolkwitz, R., and Marsson, M. 8
 Krieger, W. 8
 Lakes, classification. 29
 physiographical study. 10, 29
 Lemmermann, E. 57
 Lepadella. 59
 Leptodora kindtii. 16, 33, 43, 44
 Levels of water. 20, 25, 50, 52
 Light. 53
Limnocalanus macrurus. 31, 32
 Limnoplankton. 8
 Lohmann, H. 37
 Long Lake. 31
 Lulu Lake. 36
 Lyngbia. 46
Lysigonium granulatum. 15, 16, 18, 31
 McIntyre Lake. 25
 Macon Lake. 25
 Marsh, C. D. 22, 30, 31, 32
 Mendota, Lake. 31, 46, 54
 Methods. 11
 Michigan, Lake. 31, 32, 34, 35, 46, 52
Microcystis aeruginosa. . . . 14, 16, 18, 44, 46
 Minnesota, Lakes. 26
 Mississippi River. 14, 17, 30, 57, 58
Moina brachiata. 59
 micrura. 16, 44, 59
 Monostyla. 27, 59
 lunaris. 35
 Murray, James. 26
 Mysis. 32
 Naumann, E. 8
 Nordquist, Harald. 33
Notholca longispina. 31, 32, 33, 59
 striata. 16, 21, 27, 31, 32, 39
 40, 44, 46, 59
 Obligoplankton. 8
 Oconomowoc Lake. 31, 35
 Oder River. 51
 Ohio River. 14
 Oxbow pond, Urbana. 26
 Oxygen. 12, 18, 23, 24, 27, 39, 54, 56
 Paraguay. 57
 Patagonia. 57
 Pearsall, W. H. 55
 Pecatonica River. 21
Pedalia mira. 15, 16, 33, 44, 57
Pediastrum duplex. 14, 31, 40, 44, 59
 Pepin, Lake. 19, 30, 57
 Pernod, M. 57
 Perennials. 10, 21, 39, 44
 Pewaukee Lake. 36
Phacus longicauda. 16, 44
 Plankton, classification. 8, 57
 counting. 11
 definition. 7, 8
 development. 47
 ecological classification. 57
 geographical distribution. 57
 lakes. 22, 29
 stable streams. 13
 temporary ponds. 26
 young streams. 19
 Playfair, G. I. 57
Pleodorina illinoisensis. 18, 19, 48
 Polyarthra. 30, 33, 35
 platyptera. 33
 trigla. 14, 15, 16, 18, 31, 33
 34, 36, 39, 44, 57, 59
 Ponds, Decatur, Illinois. 23, 39, 55
 Gary, Indiana. 28, 35
 Inverness, Mississippi. 24
 Mineral, Illinois. 24
 Monticello, Illinois. 28
 Mt. Carmel, Illinois. 24
 Neosha, Wisconsin. 24
 Urbana, Illinois. 24, 39, 55
 Pontoporeia. 32
 Predominants. 57, 58

- Predominants, deep lakes.....29, 46, 59
 - definition.....7, 9
 - estival.....44
 - hiemal.....44
 - Lake Decatur.....18
 - perennial.....44
 - ponds.....24, 26, 35, 37, 45, 59
 - seasonal.....36
 - serotinal.....44
 - stable streams.....16, 59
 - vernal.....44
- Prevalents.....7, 9
- Protozoa.....14, 27, 31, 51
- Purdy, W. C.....14
- Reelfoot Lake.....24
- Rheoplankton.....8
- Richardson, R. E.....14, 16
- Rock River.....15, 17
- Rotifers.....14, 15, 27, 30, 31, 57, 59
- Russian waters.....59
- Rylov, V. M.....8
- Salt content.....24, 55
- Salt Fork.....21, 26
- Sand Lake.....31
- Sandon, H.....57
- Sangamon River...17, 20, 45, 48, 49, 53, 55
- San Joaquin River.....17, 52
- Scenedesmus quadricauda*...14, 16, 27, 31
- Schizocerca diversicornis*.....33
- Schroder, B.....51
- Schröter, C.....57
- Seasonals.....10, 21, 36
 - glacial lakes.....46
 - perennial ponds.....37, 44
 - stable streams.....37, 44
- Shelford, V. E.....10, 34, 54
- Shelford, V. E., and Eddy, S.....7
- Shackleford, Martha.....26
- Simocephalus.....27, 35, 59
- Smith, Frank.....34
- Smith, G. M.....8
- Smith, V. G.....7, 43
- Socias, autumnal.....43, 46
 - bottom.....28
 - estival.....43, 46
 - hiemal.....39
 - pelagic.....28, 59, 60
 - seasonal.....7, 36, 45
 - serotinal.....43
 - stratal.....5, 8
 - vernal.....39, 46
- Society, pelagic.....8, 9, 60
 - seasonal.....36
 - stratal.....8
- Spoon River.....21
- Stenoeccius species.....7, 58
- Stentor.....39
 - coeruleus*.....16, 44
- Stevens Creek.....21
- Streams, physiographic study.....10, 13
 - stable streams.....16, 59
 - young streams.....19
- Striatella fenestrata*.....31, 32, 59
- Succession.....19, 47
- Superior, Lake.....31, 32
- Synchaeta.....30, 59
 - pectinata*.....16, 33, 44, 45
 - stylata*.....16, 31, 44, 46
- Synura wella*.....16, 27, 39, 44, 46
- Tamarack bogs.....25
- Temperature.....12, 18, 20, 23, 24, 26
 - 27, 34, 39, 51, 56
- Temporary ponds.....26, 45
- Thienemann, A.....22
- Thompson, D. H.....17
- Thompson Lake.....25
- Three Mile Lake.....25
- Tintinnidium fluviatilis*.....16, 44
- Trachelomonas.....21
 - volvocina*.....15, 16, 27, 44
- Triarthra longiseta*.....33, 57
- Trochosphaera aequatorialis*.....28
- Turbidity.....12, 53
- Van Oye, P.....51, 57
- Velocity.....52, 56
- Volga River.....57
- Wabash River.....16
- Ward, H. B.....31
- Ward, H. B., and Whipple, G. C.....34
- Weese, A. O.....18, 43
- Wesenberg-Lund, C.....8, 51, 57
- West, G. S.....34, 57
- Whipple, G. C.....22, 29
- Winkler, L. W.....12
- Winnebago, Lake.....22, 31, 32
- Wolf Lake.....24
- Yellowstone Park.....34
- Young Streams.....45
- Zacharias, O.....57

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